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A TAXONOMIC REVISION OF THE STERNOPTYCHID GENUS *POLYIPNUS* (TELEOSTEI: STOMIIFORMES) WITH AN ANALYSIS OF PHYLOGENETIC RELATIONSHIPS

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ABSTRACT

The benthopelagic fish genus *Polyipnus* (Family Sternoptychidae Günther) is taxonomically revised and the phylogenetic relationships of the species investigated. Examination of specimens from most major world collections leads to recognition of 30 species for which a key is provided. New species are described from the South China Sea, off the northwestern coast of Australia, the Andaman Sea (eastern Indian Ocean), the western Indian Ocean off Kenya, and the western North Atlantic. A study of phylogenetic relationships, based on mainly osteology and photophores, resulted in a well-resolved phylogeny. Monophyly of the genus and four species groups is indicated; species complexes of earlier authors, not defined on the basis of shared, derived characters, are abandoned. Species that were previously members of the *laternatus* species complex do not constitute a monophyletic group and are now placed in the *asteroides* and *omphus* species groups with their respective closest relatives. The remaining *meteori* and *spinosus* groups contain species previously referred to the *asteroides* and *spinosus* complexes. Many new records are reported for most previously recognized species. *Polyipnus meteori* and *P. omphus* which were previously thought endemic to the western Indian Ocean are found to be widespread in the Indo-Pacific. Most species distributions remain limited even with the advent of the new material.

There have been two generic revisions of the benthopelagic fish genus *Polyipnus,* family Sternoptychidae, in recent times. Schultz (1961), Baird (1971), and subsequent descriptions have brought the number of species in the genus to 25. In this revision, 30 species are recognized, 5 of which are described as new. Included are remarks on an undescribed species from the Coral Sea, herein referred to *Polyipnus* sp. B, which will be described in a separate publication by Last and Harold (submitted MS). Material from about 30 museums and institutions forms the basis of the present account. Alcohol-preserved as well as cleared and stained specimens were examined towards a phylogenetic analysis of the genus based on morphological characters.

The Sternoptychidae is a group of small luminescent fishes inhabiting mesopelagic to bathypelagic realms. Since Günther (1864) there has been much debate concerning which stomiiform genera should be placed in this family. Baird (1971) explicitly defined the Sternoptychidae and restricted it to the deep-bodied hatchetfishes including species of *Argyopelecus* Cocco, *Sternoptyx* Hermann and *Polyipnus* Günther. The family was expanded by Weitzman (1974, 1986a) to include *Araiophos* Grey, *Argyripnus* Gilbert and Cramer, *Danaphos* Bruun, *Maurolicus* Cocco, *Sonoda* Grey, *Thorophos* Bruun (including *Neophos* Myers) and *Valenciennellus* Jordon and Evermann on the basis that these 10 genera constituted a monophyletic group. The reader should consult these works for a historical background of familial composition. The subgroup including only the three hatchetfish genera is monophyletic, according to Weitzman (1974) and Harold (1993), and is now referred to the tribe Sternoptychini; see Baird (1986) and Weitzman (1986b).

Polyipnus was proposed by Günther (1887) for a single specimen of *P. spinosus,* captured by bottom trawl near the Philippines by H.M.S. CHALLENGER. Günther recognized that his specimen had affinities with the other hatchetfish

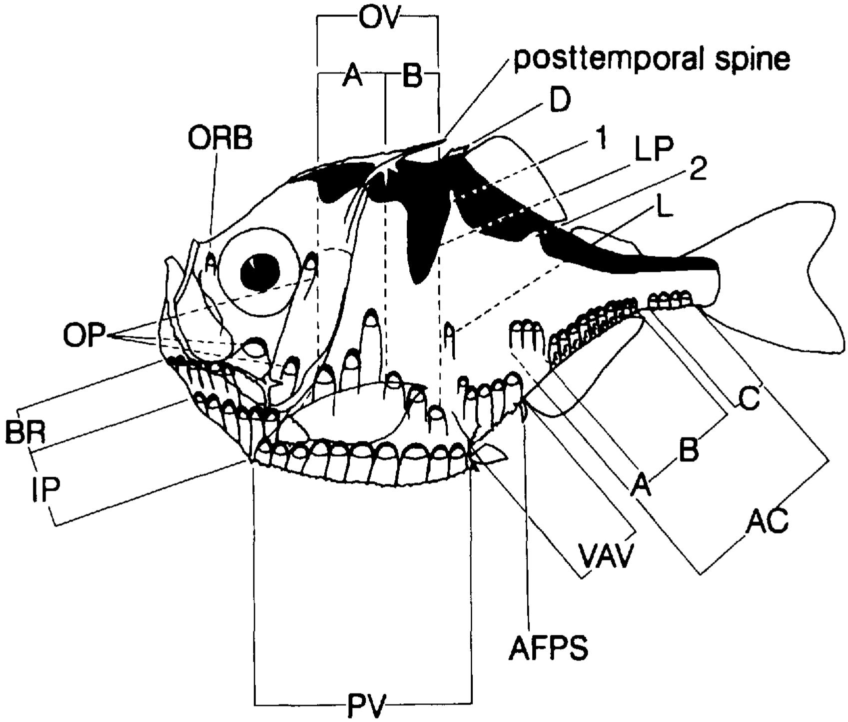

Figure 1. Photophores and other external features of *Polyipnus* species. AFPS, anal-fin pterygiophore spine; D, external, spinous dorsal process (modified dorsal-fin pterygiophore); LP, lateral pigment bar; 1, predorsal pigment notch; 2, postdorsal pigment notch. Photophore terminology, with terms of other authors in parentheses: AC, subdivided into ACA (=SAN), ACB (=AN) and ACC (=LSC and SC); BR (BR); IP (=IS and I); L (L); OP (=PRO + PTO + SO); ORB (=PO); OV, subdivided into OVA (=SP) and OVB (=SAB); PV (AB); VAV (=PAN).

genera, *Argyropelecus* and *Sternoptyx,* but noted some important distinctions. Diagnostic features were the multispinose posttemporal bone and the large number of ventral photophores posterior to the anal-fin origin (=AC) (Fig. 1). The next *Polyipnus* species described, *P. laternatus* Garman (1899) from the North Atlantic Ocean, was distinguished by a single posttemporal spine (Fig. 2) (compared with 3 in *P. spinosus*) and the absence of spinelike denticles originating on the modified ventral photophore scales. The species both had 10 abdominal photophores with associated heavy scales forming a ventral bony keel.

Shortly after the turn of the century three species similar to *Polyipnus spinosus* from the Pacific Ocean were described: *P. stereope* Jordan and Starks (1904) from Sagami Bay, Japan; *P. nuttingi,* Gilbert (1905), Hawaiian Islands; and *P. tridentifer* McCulloch (1914), Great Australian Bight. *Polyipnus fraseri* Fowler (1934) from off the Philippines was the next to be described and, although it shared many unusual features with *P. spinosus* and allies which are not present in *P. laternatus,* a new subgenus, *Acanthopolyipnus,* was proposed for *P. fraseri.* Fowler's enigmatic species was synonymized with *P. tridentifer* and *P. spinosus* in two relatively recent reviews, Baird (1971) and Borodulina (1979) respectively, but Harold (1990b) resurrected *P. fraseri,* arguing that some of the characters considered problematical and not important by Borodulina (1979) are paedomorphic and derived.

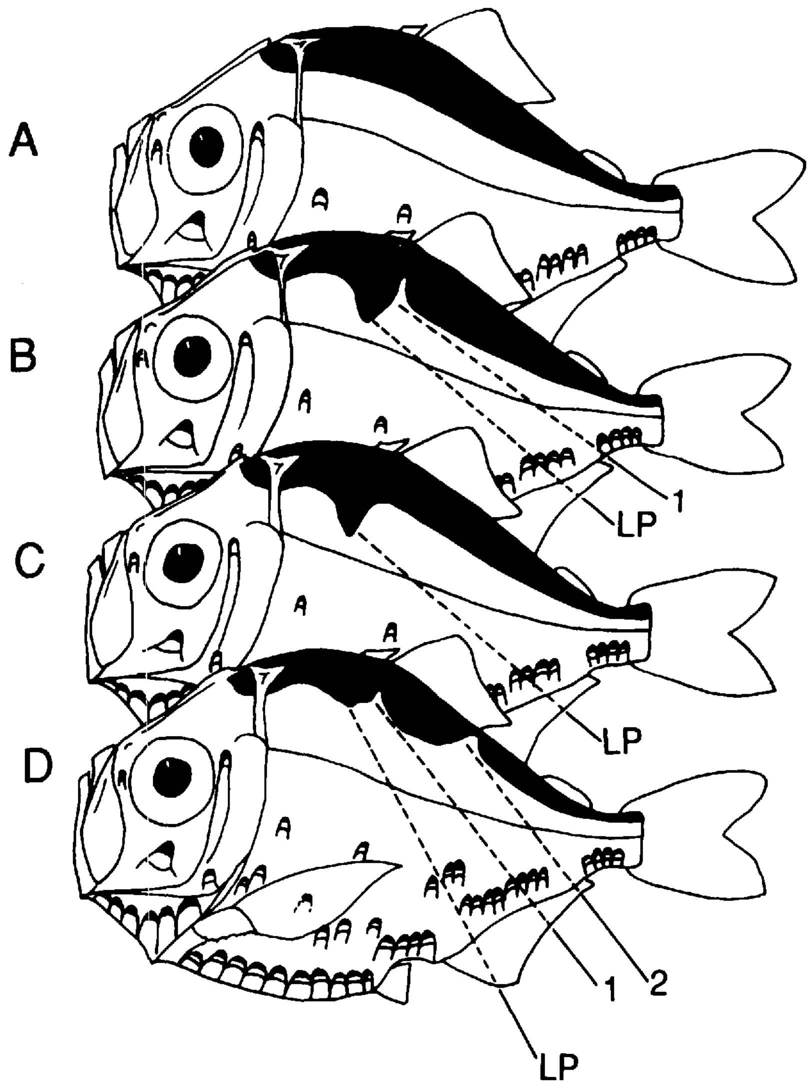

Figure 2. Diagramatic representation of dorsal pigmentation patterns in *Polyipnus* species. A, *P. unispinus*; B, *P. clarus*; C, *P. tridentifer*; D, *P. ruggeri*. Symbols defined in Figure 1 caption.

Schultz (1938) provided the first review of *Polyipnus*, and described 3 new species, *P. asteroides* (western North Atlantic Ocean), *P. unispinus* and *P. triphanos* (both Philippines). In 1961 Schultz revised the genus again, adding the new species *P. matsubarai* (Japan), *P. polli* (eastern South Atlantic Ocean), *P. indicus* (off the east coast of southern Africa) and *P. japonicus* (Japan).

Baird (1971) described five new species: *Polyipnus omphus* (western Indian and central Pacific oceans), *P. aquavitus* (Tasman and Banda seas), *P. kiwiensis* and *P. ruggeri* (off New Zealand) and *P. oluolus* (Marshall Is.). Baird (1971) subdivided *Polyipnus* into three species complexes: the *asteroides* complex (*asteroides, kiwiensis, matsubarai, meteori, polli, ruggeri* and *triphanos*), the *laternatus* complex (*aquavitus, laternatus, omphus* and *unispinus*) and the *spinosus*

complex (*indicus, nuttingi, oluolus, spinosus, stereope* and *tridentifer*). Within the *P. spinosus* complex Baird recognized a subgroup with 1 or 2 posttemporal spines and low anal (=ACB) photophore number, referred to the *P. indicus* subgroup by Borodulina (1979) and another with 3 posttemporal spines with relatively high anal photophore number, the *P. spinosus* subgroup.

Of the three species complexes established by Baird (1971), only the *Polyipnus spinosus* complex has attracted much systematic investigation. Borodulina (1979) reviewed the *P. spinosus* subgroup, describing three new species: *P. parini* (western Pacific Ocean), *P. elongatus* (Coral Sea) and *P. spinifer* (off the Philippines and Japan). Later she added *P. inermis,* a new species from the Sala-y-Gomez Ridge, eastern South Pacific Ocean (Borodulina, 1981). This was the first record of *Polyipnus* from the eastern Pacific. More recently, a new species from the Coral Sea in the *P. spinosus* complex, *Polyipnus paxtoni* Harold (1989), was described. Harold presented evidence for monophyly of the *spinosus* complex but recommended that further subdivisions of the complex should not be recognized until phylogenetic relationships are better understood.

Recent additions to the other two species complexes recognized by Baird (1971) have also been proposed. Harold (1990a) described a new miniature species, sensu Weitzman and Vari (1988), most similar to *P. unispinus,* from the South China Sea. The new species *P. danae* Harold (1990) was provisionally assigned to the *laternatus* species complex of Baird (1971) with the caveat that homoplasy obscured interrelationships. *Polyipnus surugaensis* Aizawa (1990) was described recently based on a specimen from Suruga Bay, Japan and added to the *asteroides* species complex. This species is thought to be most similar to *P. triphanos* of the Indo-Australian Archipelago.

Baird (1971) was the first to propose relationships among groups of Recent *Polyipnus* species, although the genus had been previously reviewed. Members of the *spinosus* species complex were considered most primitive on the basis of generalized axial and caudal osteology. The remaining *asteroides* and *laternatus* complexes were thought to be most closely related, having similar body form, posttemporals, photophore configuration and dentition. Some of the characters identified by Baird are not derived with regard to *Polyipnus* and as such are not regarded here as evidence of most recent common ancestry.

I adopt the analytical methods of Hennig (1966) and Wiley (1981), phylogenetic systematics, in which only shared derived characters (synapomorphies) are evidence of common ancestry or monophyly and only monophyletic groups are recognized as valid taxa. In this study I analyze a suite of morphological characters and propose phylogenetic relationships for the 30 *Polyipnus* species, with some preliminary analysis of *Polyipnus* sp. B. The only known specimen of *Polyipnus surugaensis* Aizawa (1990) was not available for study: tentative phylogenetic placement is made based on the description provided by Aizawa (1990).

Materials and Methods

Specimen Sources.—Specimens were made available for this study from museums and institutions around the world. The names and standard abbreviations of these sources follow Leviton et al. (1985). Specimens studied are listed by museum catalog number in each species account. Collection data are provided for uncataloged material consisting of number of specimens, size range in mm standard length, latitude and longitude, depth of tow, sounding depth (S.D.), vessel, local time and date when available. In some cases, especially expeditions of the DANA, only the length of the wire in mwo (meters of wire out) was available.

Descriptive Methods.—Over the last 30 years a set of unique terms and abbreviations was used to refer to the various photophores of the deep-bodied sternoptychids, e.g., Schultz (1961) and Baird

(1971). Weitzman (1974) synonymized such terms with the homologous counterparts in common use for all other stomiatoid (=stomiiform) fishes, although he was uncertain as to the equivalents of supra-anal (SAN) and lateral (L) photophores. Badcock (1984) used the new terminology in a key to the hatchetfishes of the eastern Atlantic; this appears to be the only application until Ahlstrom et al. (1984) and Weitzman (1986) further improved the terminology based on developmental information.

To facilitate outgroup comparisons among stomiiforms in phylogenetic analysis I apply the system of photophore terminology presented by Ahlstrom et al. (1984) and Weitzman (1986a), with modifications, to the hatchetfishes (Fig. 1) (the superceded terms of Schultz, 1961 are given in parentheses): AC, ventral and extending from anal-fin origin to caudal-fin base, subdivided into ACA (=SAN, supra-anal), ACB (=AN, anal) and ACC (=LSC and SC, subcaudal); BR, photophores on branchiostegal membranes; IP (=IS and I, isthmus), ventral photophores on the isthmus; L, lateral photophore dorsal to pelvic-fin base, immediately ventral to lateral midline; OP (=PRO, preopercular + PTO, postorbital + SO, subopercular), photophores associated with the opercular bones; ORB (=PO, preorbital), photophore immediately anterior to the orbit; OV, flank photophores between operculum and pelvic-fin base, subdivided into anterior OVA (=SP, suprapectoral) and posterior OVB (=SAB, supra-abdominal); PV (=AB, abdominal), ventral photophores between pectoral-fin base and pelvic-fin base; VAV (=PAN, preanal), ventral photophores between the pelvic- and anal-fin origins.

There is morphological evidence that the ACA/supra-anal photophores are equivalent to the AC of other stomiiforms. The ACA (supra-anal) photophores develop from the ACB (anal) group by a budding process (pers. obs.) in most *Polyipnus* species ("white" development, Ahlstrom, 1974, was observed for members of the *asteroides* species group). On the basis of Hennig's (1966) ontogenetic criterion the supra-anal photophores therefore are AC homologues. Topographically the ACA are equivalent to anterior AC photophores of other sternoptychids and of gonostomatids, being located in the first three myotomes of the anal fin. Five discrete arrangements of ACA occur in *Polyipnus* (Fig. 3). In adults of some species (e.g., *P. tridentifer*) the third ACA photophore is united with the ACB section (Fig. 3A). The homology of the L (="lateral") photophore of *Polyipnus* remains uncertain and therefore the unique term is retained.

I make a change to the equivalence of orbital (ORB) and opercular (OP) photophores of deep-bodied sternoptychids with other stomiiforms, following Badcock (1984). Ahlstrom et al. (1984) list in their table 51 that *Polyipnus*, *Sternoptyx* and *Argyropelecus* are all characterized by 2 ORB and 2 OP. In fact, the photophore traditionally called "postorbital" (PTO) in hatchetfishes is the homologue of the superior opercular photophore present in most stomiiforms. In both instances this photophore is located near the dorsal extremity of the preopercle. Posterior opercular photophores of photichthyans are located on the cheek in association with the infraorbital bones. The adult complement for the three deep-bodied sternoptychid genera is, therefore, the same as in most other sternoptychids and gonostomatids: ORB 1 and OP 3.

In the accounts numbers in parentheses indicate the number of photophores in a common organ. For example, ACA 1 + (2) indicates that in the anteriormost AC group there is 1 isolated photophore followed posteriorly by 2 united in a common organ. The position of a photophore in a given group or cluster is indicated by its number in sequence, counting from the anterior. Other important photophore terminology related to the presence (Fig. 4A, C) or absence (Fig. 4B) of denticles on the scales that cover the photophores and whether the ventral reflector parts of the ACC photophores are separated by broad gaps (Fig. 4D) or in close proximity (compact) (Fig. 4E).

A bilaterally symmetrical bony structure is present at the leading edge of the dorsal fin in *Polyipnus* species (Fig. 1). This was referred to as a dorsal blade by Schultz (1961) and others but the use of the term may invite inappropriate outgroup comparisons with superficially similar structures in *Sternoptyx* and *Argyropelecus*. The dorsal blade of the last two genera is made up of a single modified supraneural in *Sternoptyx* or seven supraneurals in *Argyropelecus*. In *Polyipnus* the paired bladelike structure is an external projection of one or two fused pterygiophores and possibly a supraneural, according to Weitzman (1974). In the present account, the structure in *Polyipnus* will be referred to as the dorsal spinous process and the associated spines as dorsal spines (D in Fig. 1).

A pair of ventrolaterally-directed spines which originate on the first anal-fin pterygiophore is present in some species (AFPS in Fig. 1). There has also been some confusion in the literature concerning terminology for spines and spinelike extensions of scales. I follow Schultz (1961) in using the term denticle for structures originating on the platelike scales that cover the ventral photophores.

All species of *Polyipnus* have between one and three posttemporal spines of various sizes and configurations (Figs. 1, 5). The most complex arrangement is shown in Figure 5A in which there are dorsal (d), median (m) and ventral (v) spines. Some species have reduced ventral and median posttemporal spines which could be confused with serrations: for example, see Harold (1989: fig. 1), *P. paxtoni*. Spines are distal projections of ossified rods that originate near the structural base of the dorsal posttemporal spine. Serrations are confined to the margins of bony structures. The two-spined configuration (Fig. 5B) has long dorsal and short basal (b) spines. The simplest arrangement, shown in Figure 5C in a modified elongate form, is the unispinous posttemporal. Some unispinous species

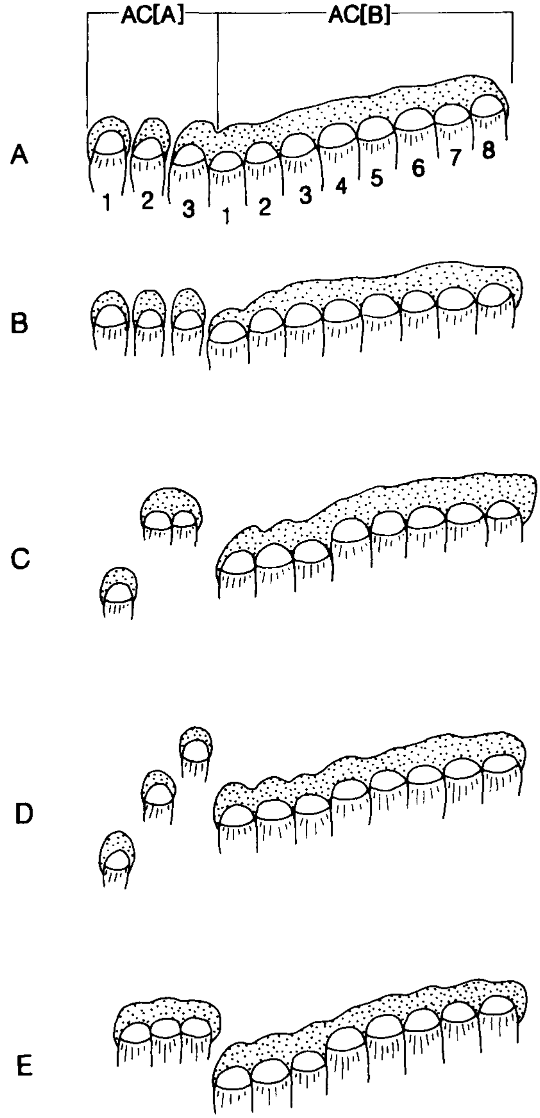

Figure 3. Configurations of ACA photophores and their topographical relationships to ACB, left side: A, ACA 1 + 1 + 1, horizontal with third joined to first ACB (e.g., *P. indicus*); B, ACA 1 + 1 + 1, horizontal with third not joined to ACB (e.g., *P. omphus*); C, 1 + (2) with second and third united and highly elevated (e.g., *P. asteroides*); D, 1 + 1 + 1, increasing in elevation anterior to posterior, third highly elevated relative to first ACB (e.g., *P. meteori*); E, ACA (3), horizontal and united but not joined to first ACB (e.g., *P. bruuni*).

have an anterodorsal barb at the base of the posttemporal spine. There are various spines located at the preopercular angle, occurring in up to three positions. The ventral preopercular spine (VPS) is always the longest in *Polyipnus* and is either free of the distal lamella (Fig. 6A) or embedded within it (Fig. 6B). A large, free posterior preopercular spine (PPS, Fig. 6A) is present in one species (*P. fraseri*) and a dorsal spine (DPS, Fig. 6A) is variously reduced or absent.

There is interspecific variation in the form of the longitudinal parietal keel. This structure is in some species a continuous serrated blade (Fig. 6C) and in others variously differentiated but often with the posterior section modified as a pair of opposed median spines (Fig. 6D).

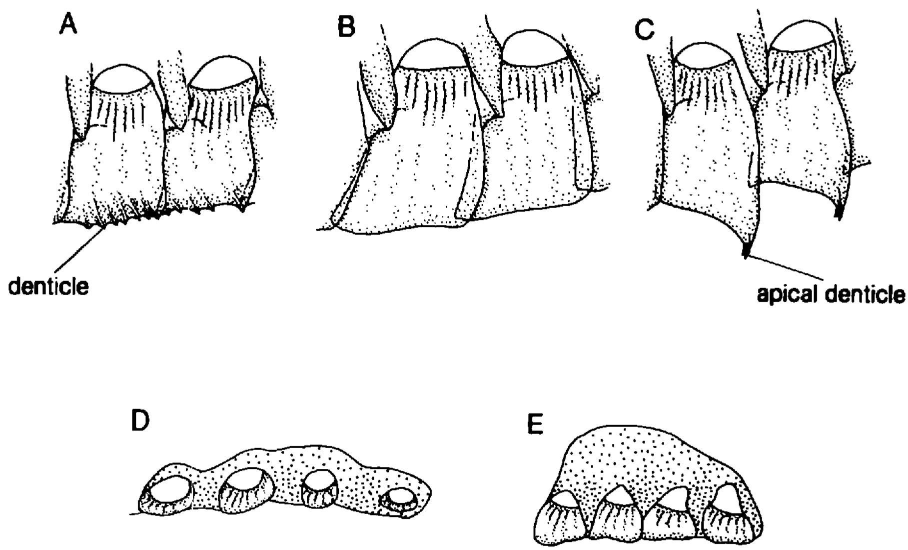

Figure 4. Photophore denticulation and spacing, left side: A, ventral margin with numerous denticles; B, ventral margin smooth, nondenticulate; C, ventral margin with triangular margin and apical denticle(s); D, photophore reflectors separated by broad gaps; E, photophores compact, reflectors not separated by broad gaps.

Most *Polyipnus* species have a continuous saddle of dark pigment (Figs. 1, 2) with a diagnostic pattern of ventral undulations. There is usually a fingerlike lateral bar (LP in Figs. 1, 2) of pigment extending ventrally immediately anterior to the dorsal fin. There may also be a notchlike dorsal deflection of the pigment margin ventral to the dorsal-fin origin (predorsal pigment notch: 1 in Figs. 1, 2) and/or ventral to the insertion (postdorsal pigment notch: 2 in Figs. 1, 2). Definition of these pigmentation features is critical to diagnoses and to the analysis of phylogenetic relationships presented.

Unless indicated otherwise, determinations of morphometric and meristic characters were made following Hubbs and Lagler (1958). Some measurements are not homologous from point to point and information derived from them is not used in the phylogeny. All fish lengths are standard lengths. The total number of fin rays is given. Vertebral counts are the total number and are determined from x-radiographs. Values of meristic characters (excluding photophores) for holotypes are given in parentheses. Head length is the distance from the tip of the snout to the most distal border on the operculum; orbit length is the diameter of the orbit in the horizontal plane; body depth is always the maximum; caudal-peduncle depth is the minimum; caudal-peduncle length is the distance from the posterior anal-fin ray to the structural base of the central caudal-fin ray; predorsal length is the distance from the origin of the dorsal fin to the tip of the snout; dorsal-fin length and anal-fin length are basal lengths; preanal, predorsal and preventral lengths are the distance from the tip of the snout to the anterior anal-fin, dorsal-fin and pectoral-fin rays, respectively; postdorsal and postanal lengths are the distance from the origins of the dorsal and anal fins, respectively, to the end of the vertebral column. ACC length is the maximum distance from the anterior margin of the platelike scale covering the ventral reflector, see Herring and Morin (1978, and references therein), to the posterior margin of the corresponding scale of the posteriormost ACC photophore. ACB-C length is the minimum distance between covering scales of the ACB and ACC photophore clusters. ACA elevation is the distance from the dorsalmost point of the third ACA photophore to the equivalent position on the first ACB.

The term scale is used here for the platelike structures covering the reflectors of the ventral photophores. These plates are the modified ventral extremities of the lateral surfaces of "cycloid" scales of the ventrolateral surface of the body. The insertion, imbrication and presence of circuli all suggest that the scales of *Polyipnus* and other stomiiforms are true scales. The term "cycloid," however, is not used here to reflect homology with similar scales in fishes other than stomiiforms: these generally unornamented scales appear to have been derived several times during the evolutionary history of teleosts; see Roberts (1993).

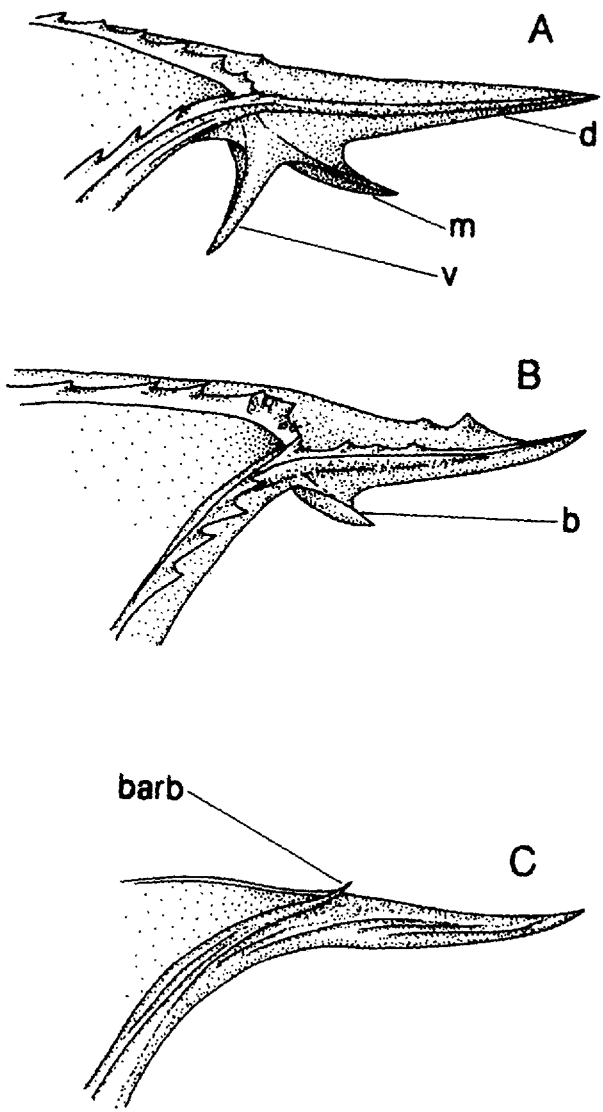

Figure 5. Posttemporal spine configurations and terminology, left side: A, three spines, d = dorsal, m = median, v = ventral; B, two spines, b = basal (median/ventral); C, single spine with anterodorsal barb.

Phylogenetic Methods.—Outgroup comparison: According to Weitzman's (1974) phylogenetic analysis, a clade consisting of *Sternoptyx* and *Argyropelecus* is the sister group to *Polyipnus*. These "hatchetfish" genera are the sister group to a clade comprising *Argyripnus* and *Sonoda*. This well-corroborated set of relationships forms the framework for establishing the polarity (plesiomorphic/apomorphic status) of characters within *Polyipnus* by outgroup comparison (Wiley, 1981; Watrous and Wheeler, 1981). *Argyripnus atlanticus* Maul and *Argyripnus* sp. (*A.* aff. *ephippiatus* Gilbert and Cramer) were cleared and stained using the counterstaining procedure for bone and cartilage. Cleared and alizarin-stained specimens of *Sonoda megalophthalma* Grey and *Thorophos euryops* Bruun in the USNM collection were also studied. I refer to Weitzman's (1974) descriptions and illustrations exclusively for *Araiophos*, including text and figure references where appropriate. Of the remaining sternoptychid genera, representatives of *Danaphos*, *Valenciennellus* and *Maurolicus* were also cleared and stained for checking polarities established within the five-taxon system described above. The most

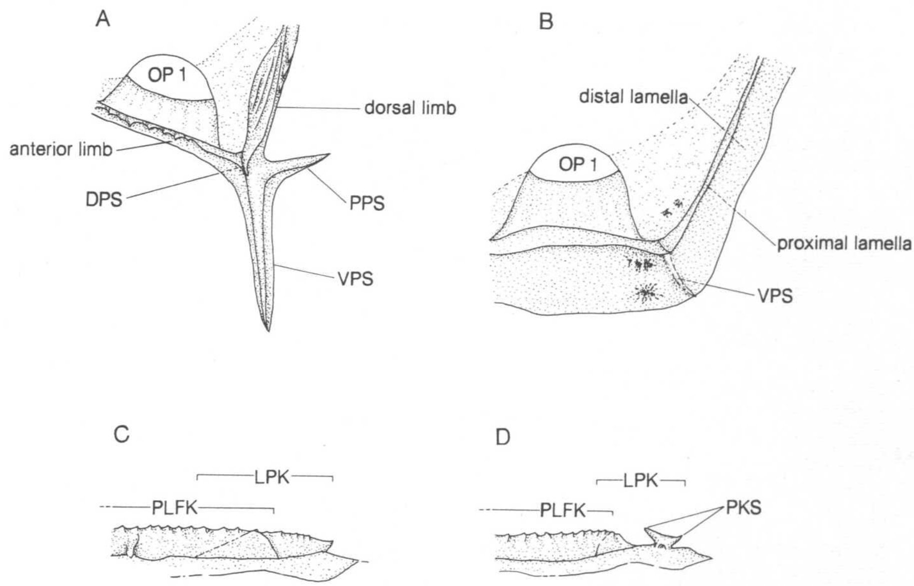

Figure 6. Terminology of preoperculum and associated spines and external longitudinal keels of frontal and parietal bones, left side: A, free ventral preopercular spine. Preopercular spines: VPS = ventral, PPS = posterior, DPS = dorsal; B, VPS reduced and embedded within distal lamella of preopercle; C, longitudinal parietal keel continuous with frontal keel: PLFK = primary longitudinal frontal keel, LPK = longitudinal parietal keel; D, LPK discontinuous, differentiated posteriorly as two opposed median spines: PKS = parietal keel spines.

probable ingroup (within *Polyipnus*) character polarities will usually be established by examining the first two outgroup branches (Maddison et al., 1984). Characters for which there were no comparable structures in the designated outgroup genera were polarized by the method of functional outgroup/functional ingroup comparison (Watrous and Wheeler, 1981; Mooi, 1989).

ANALYTICAL TECHNIQUES. The phylogenetic analysis was done manually using a computer graphic aid (Maclade software, version 2.1, written by Maddison and Maddison) on an Apple Macintosh Plus microcomputer. All characters are binary except numbers 13, 31 and 86 which are multistate and unordered. A more powerful branch-swapping algorithm was available through PAUP (Phylogenetic Analysis Using Parsimony, version 3.0, Swofford, 1990) and was used to check results and to search for more parsimonious trees (BRANCH AND BOUND option with GLOBAL branch-swapping). As an additional check, the character state matrix was analyzed with HENNIG86 (version 1.5, Farris, 1988) using the options ie- and bb in sequence. The most parsimonious cladograms, those most highly corroborated, are an estimate of phylogenetic relationships. The number of character state changes implied by the most-parsimonious cladogram and a value for CI, the consistency index (Kluge and Farris, 1969), are provided.

Of the recognized 30 *Polyipnus* species, 23 were sufficiently common in collections to allow clearing and staining. Six of the other species (*P. bruuni* n. sp., *P. fraseri*, *P. oluolus* Baird, 1971, *P. ovatus* n. sp., *P. parini* Borodulina, 1979, *P. spinosus*) were encoded into the matrix albeit with missing values for many characters. In analysing such a matrix, artificial resolution may occur at some nodes (Platnick et al., 1991; G. Klassen, pers. comm.): optimization of each character on each cladogram was examined towards eliminating this source of error. Tentative relationships are proposed for *P. surugaensis* Aizawa (material not available for study), using character data extracted from Aizawa (1990).

CHARACTERS. The characters studied included both external and internal structures. Since material for clearing and staining was not available for all species an emphasis was placed on external features. Among external characters are qualitative aspects of body shape and size, photophore configuration, ornamentation of platelike scales covering photophores, and the form of ridges/keels and spination of various bony structures. Internal structures were mainly osteological; observations were made on cleared and stained specimens and x-radiographs. Clearing and staining followed the procedure outlined by Dingerkus and Uhler (1977) and Potthoff (1984).

Dissections to expose various joints and other underlying structures were made following clearing and staining. The procedure described by Weitzman (1974) was followed to isolate the bones of the face, the pectoral girdle with posttemporal on the right side, the branchial basket with the pharyngobranchial bones of the right side and the hyoid arch of the left side.

Synapomorphies are numbered sequentially and described in the section on Phylogenetic Relationships. Autapomorphies are not marked on the cladograms except in cases where they are homoplastic, resembling a character used as a putative synapomorphy elsewhere or reversing from a more general character. The account of each character consists of a description of the derived condition followed by a paragraph on outgroup comparisons. Any homoplasy is mentioned in the first paragraph and interpreted in the context of the cladogram. In such cases the character number has a suffix, indicating that the character is homoplastic. These suffixes follow the system of Fink (1985) and are outlined below.

c: The character is parsimoniously interpreted as independently derived on two or more branches of the cladogram (convergence).
r: The character reverses at a lower level of generality.
R: The character is in its reversed state.
Rr: The character is in its reversed state and reverses again at a lower level of generality.
R1: The character has reversed twice to a condition resembling the original derived state.

SPECIMENS CLEARED AND STAINED. Cleared and stained material of *Polyipnus* species followed by outgroup taxa is listed below. Station data for *Polyipnus* lots listed here are provided in the descriptive accounts in the Taxonomic Revision section.

Polyipnus aquavitus Baird, 1971: AMS I.19761-029 (1), 29.0 mm; AMS I.19762-002 (1), 23.4 mm; AMS I.20316-005 (1), 29.0 mm; LACM 44493 (1), 28.1 mm.
P. asper n. sp.: USNM 304746 (2), 47.0 and 50.0 mm.
P. asteroides Schultz, 1938: CAS 61110 (1), 58.0 mm; USNM 295951 (1), 53.9 mm.
P. clarus n. sp.: ROM uncat. (1), 27.0 mm; MCZ 66696 (1), 22.0 mm; USNM 304745 (2 paratypes), 40.3 and 44.0 mm.
P. danae Harold, 1990: ZMUC P208577 (1 paratype), 24.8 mm.
P. elongatus Borodulina, 1979: AMS I.21795-007 (2), 63.0 and 65.0 mm.
P. indicus Schultz, 1961: ROM uncat. (2), 50.0 and 53.6 mm.
P. cf. *indicus*: USNM 316316 (2), 31.8 and 38.0 mm.
P. inermis Borodulina, 1981: ROM uncat. (2), 48.9 and 49.4 mm.
P. kiwiensis Baird, 1971: AMS I.15984-002 (1), 48.6 mm; AMS I.17861-001 (1), 84.0 mm.
P. laternatus Garman, 1899: MCZ 40575 (1), 33.0 mm; USNM 179050 (1), 33.9 mm; USNM 298924 (1), 43.9 mm.
P. matsubarai Schultz, 1961: ROM uncat. (1), 39.0 mm; NSMT P.12415 (1), 32.0 mm.
P. meteori Kotthaus, 1967: IOS uncat., DISCOVERY, Sta. 5415 (2), 15.7 and 29.6 mm; ZMUC P206931 (1), 37.6 mm.
P. nuttingi Gilbert, 1904: BPBM 23790 (1), 53.3 mm; BPBM 24892 (1), 39.9 mm.
P. omphus Baird, 1971: ZMUC P206933 (1), 48.0 mm; ZMUC P207116 (1), 40.0 mm.
P. paxtoni Harold, 1989: AMS I.25825-002 (1 paratype), 42.7 mm.
P. polli Schultz, 1961: MCZ 66699 (2), 21.0 and 21.4 mm; MCZ 66693 (7), 15.5–28.1 mm; ZMUC P206955 (1), 30.1 mm.
P. ruggeri Baird, 1971: AMS I.20305-009 (1), 37.0 mm; ZMUC P206957 (1), 19.6 mm; ZMUC P207118 (1), 50.3 mm.
P. soelae n. sp.: AMS I.22808-028 (2), 37.3 and 39.2 mm; AMS I.23425-011 (2), 46.0 and 60.0 mm; AMS I.22817-014 (1), 59.0 mm.
P. spinifer Borodulina, 1979: CAS 34854 (1), 49.0 mm; NSMT P.6768 (1), 38.0 mm; ZMUC P206960 (1), 66.9 mm.
P. stereope Jordan and Starks, 1904: NSMT P.6772 (1), 37.0 mm; NSMT P.6773 (1), 38.5 mm.
P. tridentifer McCulloch, 1914: AMS I.18711-014 (1), 58.0 mm.
P. triphanos Schultz, 1938: CAS 56034 (1), 27.4 mm; ZMUC P206963 (1), 30.4 mm.
P. unispinus Schultz, 1938: AMS I.19292-008 (1), 28.0 mm; ZMUC P207119 (1), 30.4 mm.

Argyropelecus species: listed in Harold (1993).
Argyripnus atlanticus Maul, 1952: FMNH 65693 (1), 55.6 mm; FMNH 71735 (1), 56.4 mm; IOS uncat., DISCOVERY Sta. 6374 (1), 44 mm.
Argyripnus sp.: MNHN uncat., Philippines (1), 87.4 mm.
Danaphos oculatus (Garman, 1899): CAS 62347 (1), 31.5 mm.
Maurolicus sp.: MCZ 66690 (2), 46.7 and 51.0 mm.
Sonoda megalophthalma Grey, 1959: USNM 201350 (1), 53.5 mm.
Sternoptyx diaphana Hermann, 1781: ROM uncat., GADUS Cr. 51 (2), 31.9 and 34.7 mm.
S. obscura Garman, 1899: MCZ 66702 (1), 19.0 mm.

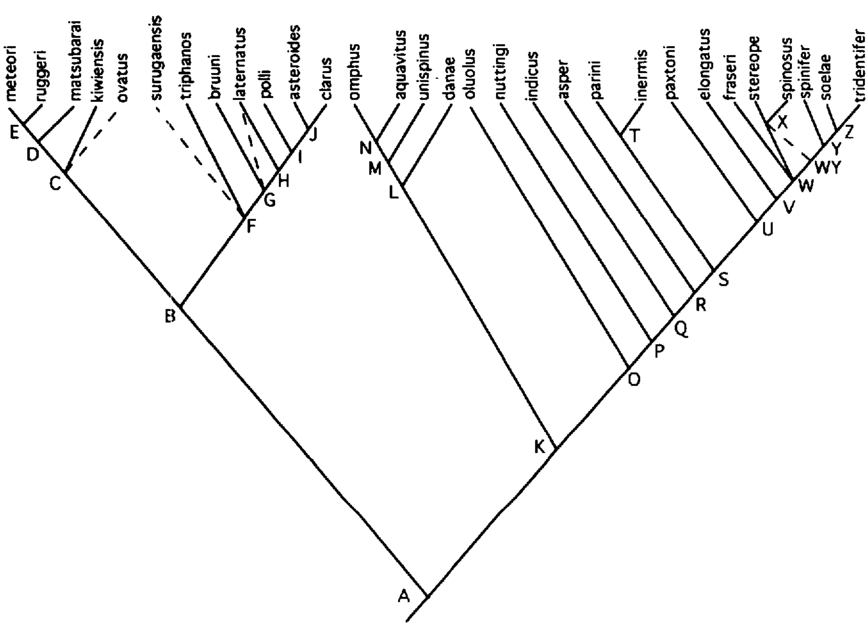

Figure 7. Cladogram depicting relationships among *Polyipnus* species. Uncertainty in branching order indicated by broken lines. See text for supporting character evidence, listed by node. Node C, *P. meteori* species group; Node F, *P. asteroides* species group; Node L, *P. omphus* species group; Node O, *P. spinosus* species group.

S. pseudodiaphana Borodulina, 1977: LACM 11293-17 (2), 25.6 and 37.3 mm.
S. pseudobscura Baird, 1971: ORIT 2115 (1), 41.1 mm.
Thorophos euryops Bruun, 1931: DANA Sta. 3736 VI (1), 44.7 mm.
Valenciennellus tripunctulatus (Esmark, 1871): MCZ 66692 (2), 21.8 and 24.9 mm.

PHYLOGENETIC RELATIONSHIPS

The phylogenetic analysis resulted in 5 equally parsimonious trees of 182 character state changes in length with a consistency index of 0.67. A single cladogram for all 30 species is provided (Fig. 7); four less-inclusive diagrams, one for each monophyletic species group, are used to map distributions of characters. Branching order within three of these groups is generally unambiguous. However, in the *spinosus* group, the Branch and Bound procedure of PAUP identified 11 cladograms only 1 step longer than the shortest tree and 62 that were only 2 steps longer. This result stems from the relatively small number of characters which apply to this group and their inconsistency. The latter is attributed to character convergence, reduction and other sources of error in proposing homology. The relationships of species within the *spinosus* group are therefore not highly corroborated.

The five equally parsimonious cladograms differ only in the position of *P. ovatus* within the *meteori* group. These different resolutions are apparently artifacts (resulting from missing values) and the species is consequently placed on the cladogram in an unresolved trichotomy with the other members of the group (Node C, Figs. 7, 11).

The position of *P. laternatus* within the *asteroides* group was completely resolved by PAUP and HENNIG86. Since that resolution was based entirely on

homoplastic characters (Node H, Figs. 7 and 14, characters 33 and 34) it is more realistically collapsed into an unresolved trichotomy (Node G).

Uncertainty in branching order in the *spinosus* species group mainly concerns the terminal six-species clade of the *spinosus* group, shown as unresolved trichotomy with a possible resolution based on a reversal (Node WY, Figs. 7, 19).

A list of the recognized species arranged alphabetically within each of four species groups is given here. Descriptive accounts in this same order follow the phylogenetics section.

Polyipnus Günther, 1887
- *P. meteori* species group
  - *P. kiwiensis* Baird, 1971
  - *P. matsubarai* Schultz, 1961
  - *P. meteori* Kotthaus, 1967
  - *P. ovatus* new species
  - *P. ruggeri* Baird, 1971
- *P. asteroides* species group
  - *P. asteroides* Schultz, 1938
  - *P. bruuni* new species
  - *P. clarus* new species
  - *P. laternatus* Garman, 1899
  - *P. polli* Schultz, 1961
  - *P. surugaensis* Aizawa, 1990
  - *P. triphanos* Schultz, 1938 complex
- *P. omphus* species group
  - *P. aquavitus* Baird, 1971
  - *P. danae* Harold, 1990
  - *P. omphus* Baird, 1971
  - *P. unispinus* Schultz, 1938
- *P. spinosus* species group
  - *P. asper* new species
  - *P. elongatus* Borodulina, 1979
  - *P. fraseri* Fowler, 1934
  - *P. indicus* Schultz, 1961
  - *P. inermis* Borodulina, 1981
  - *P. nuttingi* Gilbert, 1905
  - *P. oluolus* Baird, 1971
  - *P. parini* Borodulina, 1979
  - *P. paxtoni* Harold, 1989
  - *P. soelae* new species
  - *P. spinifer* Borodulina, 1979
  - *P. spinosus* Günther, 1887 (type species)
  - *P. stereope* Jordan and Starks, 1904
  - *P. tridentifer* McCulloch, 1914

Character Analysis

Clade A: *Polyipnus* (Fig. 7)

1. The epioccipital has an extensive shelflike posterior process which forms the point of attachment for the dorsal limb of the posttemporal (e.g., *P. meteori*, Fig. 8).

Such processes are absent in other sternoptychids.

2. The anterior ceratohyal is foreshortened and compressed (e.g., *P. laternatus* and *P. asteroides*, Figs. 9A, B). Weitzman (1974) stated that in combination with the presence of a winglike blade on the dorsal surface of the anterior ceratohyal the shortness of this bone is likely synapomorphous of *Polyipnus* species. However, this very deep blade appears to be a synapomorphy of the *asteroides* species group (character 31). The dimensions of the anterior ceratohyal of at least some

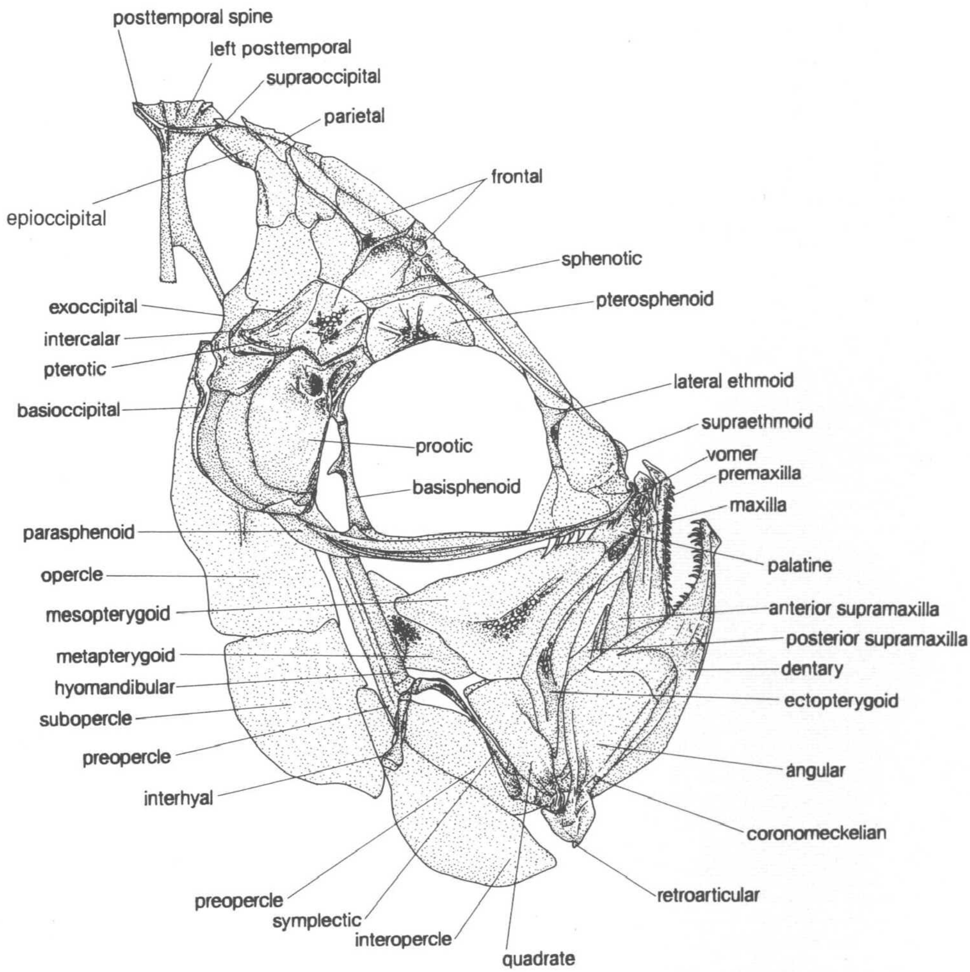

Figure 8. Cranium, right side, lateral view, and bones of the lateral and ventral regions of the head, left side, medial view: *Polyipnus meteori,* ZMUC P206931, 37.6 mm.

Polyipnus (e.g., *P. soelae,* Fig. 9C) are somewhat similar to those of *Argyropelecus* and *Sternoptyx* (see Weitzman, 1974: 405, figs. 73 and 74, resp.) and this character is therefore a questionable synapomorphy of *Polyipnus.*

The anterior ceratohyal is long and slender in all other sternoptychids and remaining stomiiforms.

3 (r). The urohyal is very large and dorsoventrally expanded (Fig. 9). A similar urohyal is present in the generalized sternoptychid *Maurolicus* sp. The urohyal is relatively small in *P. inermis,* as is the case in *Argyropelecus* species. In the context of the most-parsimonious cladogram, however, the situation in *P. inermis* is viewed as a result of secondary reduction and not plesiomorphy.

The urohyal is relatively small and not greatly expanded in other sternoptychids, especially in the first outgroup *Argyropelecus* and *Sternoptyx.*

4. Within the ACB photophore cluster there is a steplike increase in elevation immediately posterior to the third photophore (Fig. 3C, E). There is considerable

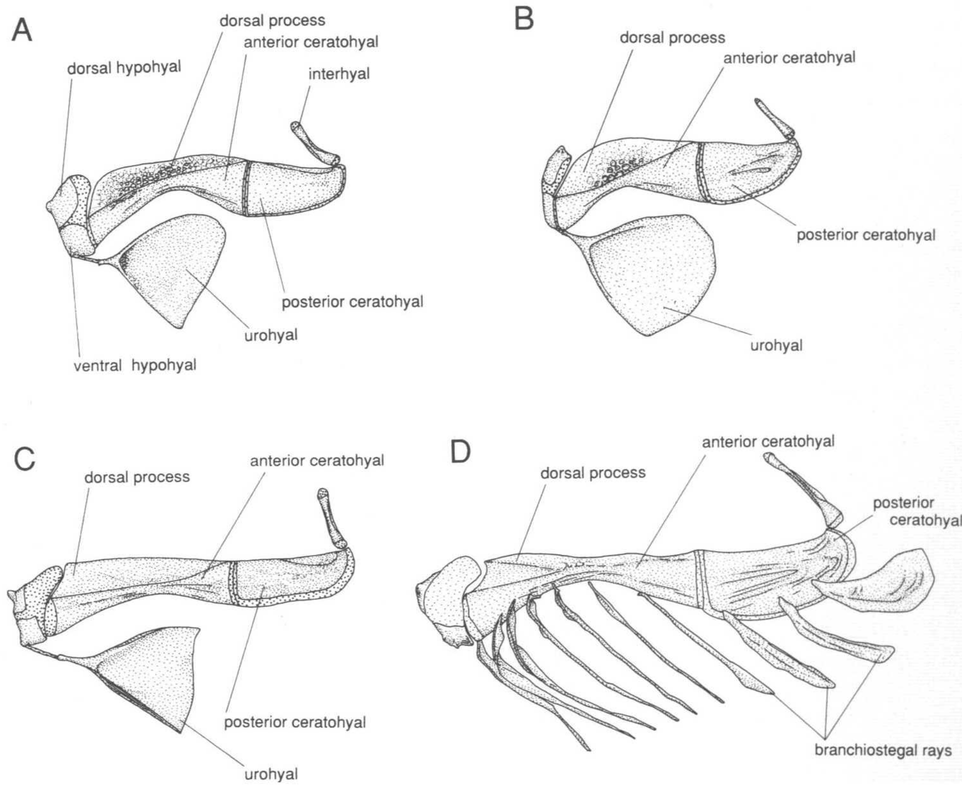

Figure 9. Hyoid arch, right side lateral view (branchiostegal rays excluded except in D): A, *P. laternatus*, USNM 179050, 33.9 mm; B, *P. asteroides*, CAS 61110, 58.0 mm; C, *P.* cf. *indicus*, USNM 316316, 38.0 mm; D, *P. soelae*, AMS I.23425-011, 46.0 mm.

interspecific variation with regard to the conspicuousness of this condition. In *P. fraseri* there does not appear to be a step which is probably a reductive feature.

5. A lateral or L photophore is present, located in the myotome immediately anterior to the first VAV photophore just ventral of the horizontal myoseptum.

No other stomiiform has such a photophore.

6. A dorsal process of the first dorsal fin pterygiophore with paired posteriorly directed spines is present in all *Polyipnus* except *P. fraseri*, a possible case of reduction. Specimens of *P. fraseri* were not available for osteological study so it remains that the process may be present but internal.

Such modification of the first dorsal fin pterygiophore is unknown in other stomiiforms. The so-called dorsal blades of *Argyropelecus* and *Sternoptyx* are modified supraneurals and not homologous to the structure in *Polyipnus*.

Clade B: *meteori* + *asteroides* species groups (Fig. 7)

7. The urohyal is rounded with a convex posterior margin (e.g., *P. laternatus* and *P. asteroides*, Fig. 9A, B, resp.).

The urohyal of other *Polyipnus* species (e.g., *P.* cf. *indicus*, Fig. 9C), and species of *Argyripnus* and *Sonoda*, illustrated by Weitzman (1974: 403, 404, figs. 70, 71), has angular posterodorsal and posteroventral margins. In *Sternoptyx* and

Argyropelecus this bone has a very deeply incised posterior margin, giving the dorsal and ventral limbs a winglike appearance.

8 and 9. The second (8) and third (9) ACA photophores are displaced dorsally relative to the first ACB (Fig. 3C, D, E). Although both are elevated in clade B the positions of these photophores are independent (Fig. 3). The second ACA may be at the same level as the third or intermediate between the first and third. There is some similarity between the configurations of the ACA photophores in *P. laternatus* which has the derived condition of both elevated and *P. omphus* in which they are nearer the elevation of the ACB, the putative plesiomorphic condition. Maybe more critical to the elevation of the respective states is that the first ACA is ventral to the second and third in *P. laternatus* although in some individuals, such as that illustrated here (Fig. 32), the vertical difference in position is slight. In *P. omphus* the ACA are usually in a horizontal line.

These photophores are closer to the elevation of the first ACB in other *Polyipnus* species. The ACA photophores of *Polyipnus* are probably homologous with parts of the VAV + ACA cluster of *Argyripnus* and *Sonoda* which are not dorsally displaced. On the basis of morphological evidence, homology of *Polyipnus* ACA with the single ACA photophore in *Sternoptyx* is uncertain because of topographical and metameric differences. However, on the basis of parsimony alone it is not possible to choose between an hypothesis of independent derivation of ACA in *Polyipnus* on the one hand and *Sternoptyx* on the other and the alternative, indicating that the presence of ACA photophores is derived at the level of the *Polyipnus-Argyropelecus-Sternoptyx* clade but lost in *Argyropelecus.*

10 (r). The ventral preopercular spine is largely or entirely embedded within the distal lamella of the preopercle (Fig. 6B). Although this character is interpreted as derived at the level of clade B, it is reversed in *P. laternatus.* In this species the spine is quite short but its terminus extends well beyond the margin of the bone and resembles the condition in the *P. omphus* species group.

A free ventral preopercular spine is present in all other *Polyipnus* species (Fig. 6A), and in all species of *Argyropelecus* and *Sternoptyx.* No other stomiiforms have such spines.

11. The OVB photophores are arranged in a "V" configuration although the relative elevations of the first and third elements vary widely in the clade. In *P. ruggeri* these photophores all approach the horizontal plane although the first and third are usually slightly elevated. In *P. laternatus* the difference in elevation between the second and third is sometimes slight but it is always present.

In most other sternoptychids, these photophores are usually in a horizontal or slightly inclined straight line (Fig. 1). The exceptions are: *P. fraseri* (*spinosus* species group) and *P. surugaensis* (*asteroides* species group) in which the posterior OVB photophore is highly elevated, and *P. oluolus* (*spinosus* species group) in which the first OVB is elevated and the second and third are ventral at about the same height. The condition in *P. omphus* resembles that of *P. oluolus* but the second photophore is always at least slightly dorsal to the third.

Clade C: *meteori* species group (Figs. 7 and 11)

12. One or two longitudinal rows of large fanglike teeth are present on an elongate posterior process of the vomer (e.g., *P. meteori,* Fig. 8).

Such teeth are absent in other sternoptychids.

13 (state 2). The ectopterygoid is elongate, narrow and curved (e.g., *P. meteori,* Fig. 8).

This bone is broad and triangular in the *asteroides* species group (e.g., *P.*

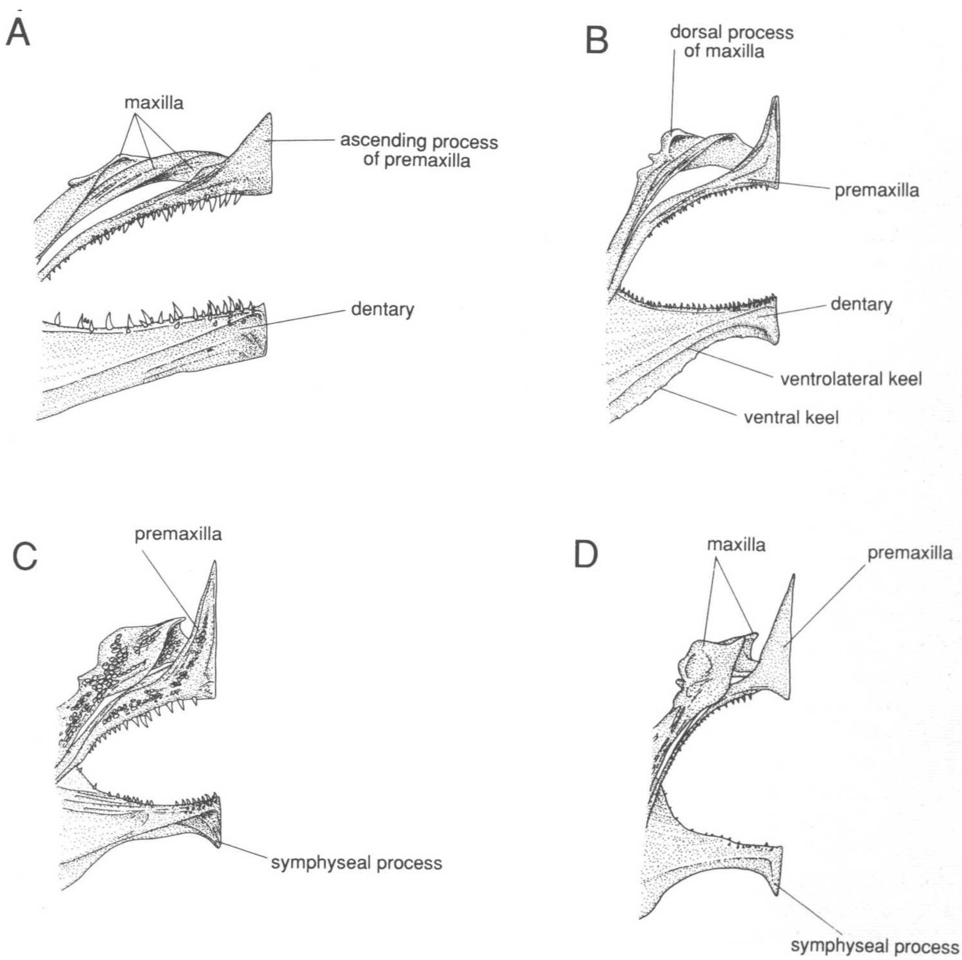

Figure 10. Anterior portions of premaxilla, maxilla and dentary, right side, lateral view: A, *P. ruggeri,* AMS I.20305-009, 37.0 mm; B, *P. omphus,* ZMUC P206933, 48.0 mm; C, *P. clarus,* USNM 304745, 44.0 mm; D, *P. laternatus,* USNM 179050, 33.9 mm.

asteroides, Weitzman, 1974: 356, fig. 30), *P. omphus* within *Polyipnus,* and in all other sternoptychids except species of *Argyropelecus* and *Sternoptyx.* In these last two genera the ectopterygoid is triangular but moderately elongate.

14. Bladelike medial processes of the posterior dorsal surface of the symplectic are inconspicuous (reduced) (e.g., *P. meteori,* Fig. 8).

These blades, which apparently contribute to the anchoring of the metapterygoid, are well-developed in all other *Polyipnus* species but absent in the remaining sternoptychids. The presence of such structures in *Polyipnus* is derived with secondary reduction in the *meteori* species group: this is the parsimonious interpretation.

15. The ascending process of the premaxilla is short and broadly triangular (e.g., *P. ruggeri,* Fig. 10A).

All other *Polyipnus* species (e.g., *P. omphus, P. clarus* and *P. laternatus* Fig. 10B, C, D, resp.), and species of *Argyropelecus* and *Argyripnus* have elongate

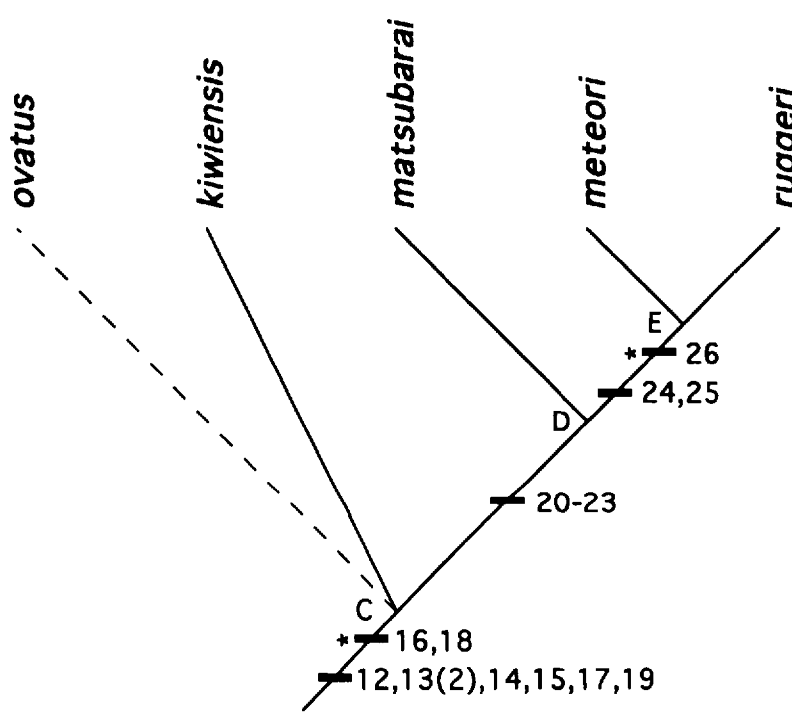

Figure 11. Cladogram depicting relationships of the *P. meteori* species group. Synapomorphies indicated by character number, cross-referenced to text. States of multi-state characters given in parentheses. Homoplastic characters indicated by '*'.

processes. The premaxilla of *Sternoptyx* species lack ascending processes, a unique condition among stomiiforms and clearly derived.

16 (R). A diagonal ridge is absent which, in other species, is present on the lateral face of the preopercle at the point of divergence of the dorsal and anteroventral limbs.

This ridge is well-defined or even prominent and spinose in other *Polyipnus* species but absent in the remaining sternoptychid genera. The present polarization is the most parsimonious one.

17. The symphyseal process of the dentary is truncate, without conspicuous ventral extension (e.g., *P. ruggeri,* Fig. 10A).

The dentary symphysis is broadly triangular in all other *Polyipnus* species (e.g., *P. omphus,* Fig. 10B) except *P. asteroides, P. bruuni, P. clarus* (Fig. 10C), *P. laternatus* (Fig. 10D) and *P. polli* in which it is moderately elongate and narrow. In species of *Argyropelecus, Sternoptyx* and *Argyripnus* the process is triangular.

18 (c). The iliac spine is very short, its length much less than that of the ischial process. Similar conditions occur in *P. laternatus* and *Argyropelecus* species which are tentatively interpreted as convergences.

The iliac spine is about equal in length to or longer than the ischial process in other *Polyipnus* species. Comparisons with other outgroups are not possible because of extreme modification in *Sternoptyx* and a lack of iliac spines in other stomiiform genera.

19. The lateral ridge of the dorsal limb of the posttemporal is finely serrate.

Such serrations are absent in all other *Polyipnus* species, and species of *Ar-*

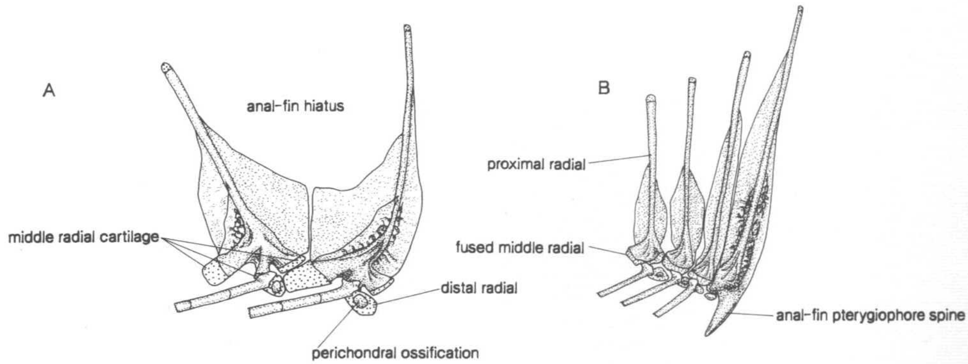

Figure 12. Anal-fin pterygiophores, right side, lateral view: A, hiatus pterygiophores, *P. meteori*, ZMUC P206931, 37.6 mm; B, anterior four pterygiophores, *P. unispinus*, AMS I.19292-008, 28.0 mm.

gyropelecus, Sternoptyx and other sternoptychid genera. Serrations are present on this ridge in most species of the *spinosus* species group but they are large, spine-like structures and probably independently derived.

Clade D: *matsubarai* to *ruggeri* (Fig. 11)

20. Middle radial cartilage of anterior anal-fin pterygiophores are deeply dissected into three separate elements (e.g., *P. meteori*, Fig. 12A). These cartilages are enveloped by ossification, producing secondary articular heads.

In other *Polyipnus* species (e.g., *P. unispinus*, Fig. 12B) and species of the other sternoptychid genera there are occasionally two cartilages, but in most cases there is just one continuous element.

21. The basisphenoid is very narrow and not particularly expanded basally (e.g., *P. meteori*, Fig. 8).

In other *Polyipnus* species the ventral shaft of the basisphenoid is relatively broad and expanded or flared towards its basal articulation with the parasphenoid. Although comparisons to the outgroups are somewhat ambiguous the most parsimonious interpretation of this character is apomorphy within *Polyipnus*. The basisphenoid is lacking in *Argyropelecus*, narrow in *Sternoptyx* but quite broad and basally expanded in *Argyripnus*.

22. The basisphenoid posteriorly-directed spinelike process is short (e.g., *P. meteori*, Fig. 8).

In all other *Polyipnus* species, and species of *Sternoptyx* and *Argyripnus* this process is long and in some cases extends well posterior to the anterior margin of the ascending limb of the parasphenoid.

23. The third infrapharyngobranchial (PB3) and its associated fused dentigerous plate (UP3) are elongate. The head of the bone articulating with PB4 is not greatly flared and the patch of teeth covers at least part of the shaft of the bone (e.g., *P. meteori*, Fig. 13A).

Plesiomorphically, the posterior head of PB3 is expanded or flared at its articulation with PB4 (e.g., *Maurolicus* sp., *Sonoda megalophthalma*, and *Polyipnus asteroides*, Weitzman, 1974: 409–411, figs. 76–78, resp.). All other *Polyipnus* species except *P. triphanos* (which lacks teeth on UP3), and species of *Argyripnus* the UP3 teeth are not present on the shaft of the bone, being restricted to the medial surface of the posterior articular head. In *Argyropelecus* species there are no teeth associated with this tooth plate. The third and fourth infrapharyngobran-

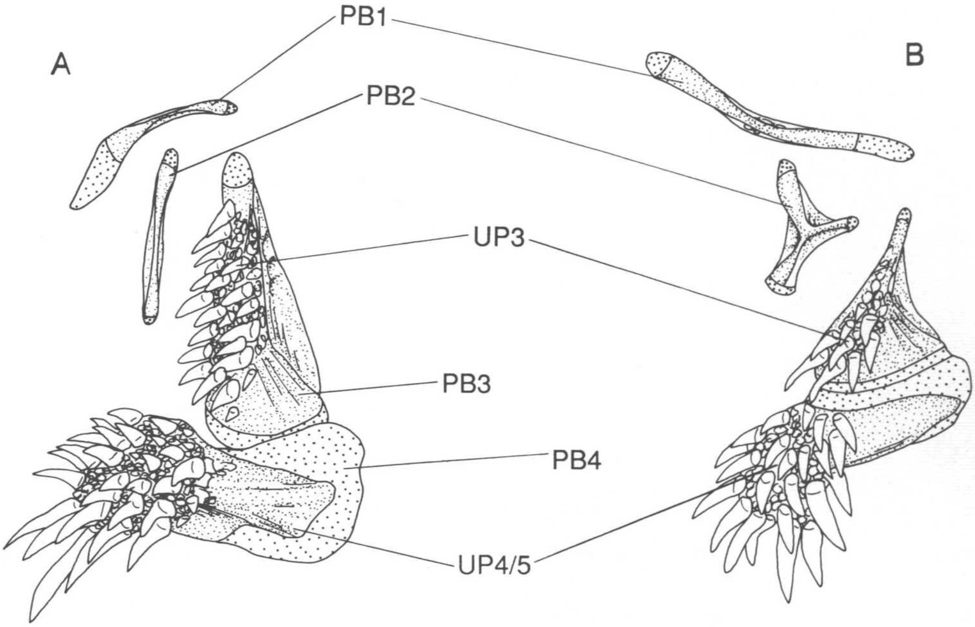

Figure 13. Infrapharyngobranchial bones and associated tooth plates, right side, medial view: A, *Polyipnus meteori*, ZMUC P206931, 37.6 mm; B, *P. clarus*, USNM 304745, 44.0 mm. Standard labels, as defined by Rosen (1973).

chials, which bear tooth plates in *Sternoptyx* species, are fused, making homology of the teeth uncertain. In any case, in *Sternoptyx* there are no teeth on the shaft of this composite element.

Clade E: *meteori, ruggeri* (Fig. 11)

24. The ventral margin of the dorsomedian body of dark pigment has an abrupt postdorsal notch, near the horizontal position of the ACA photophores, (*P. meteori* and *P. ruggeri*, Figs. 24, 26, resp.). In *P. matsubarai* (Fig. 22) there is a condition resembling that of *meteori* and *ruggeri* but it is a much more gradual deflection, especially posteriorly.

In other *Polyipnus* species, and species of *Argyropelecus* and *Argyripnus* this region of the pigment margin is either raised in a broad, shallow arc or is essentially straight as in *Maurolicus* sp. and *P. unispinus*. A dorsal body of dark pigment is not present in other outgroups.

25. The supraoccipital has a median posteriorly-directed rodlike process.

In other members of the genus there is either a median bladelike process or no process at all. This character was polarized by functional outgroup comparison since there are no equivalent structures outside *Polyipnus*.

26. Hypurals one and two are not fused. Although a similar condition exists in *Argyropelecus affinis* and *A. gigas* this is parsimoniously interpreted as convergent.

Hypurals one and two are fused in other *Polyipnus* species and members of the remaining sternoptychid genera.

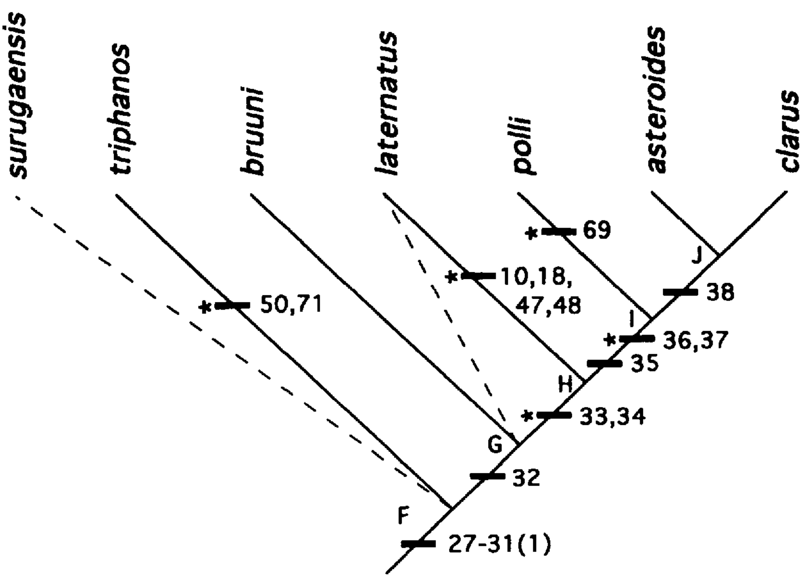

Figure 14. Cladogram depicting relationships of the *Polyipnus asteroides* species group. Conventions defined in Figure 11 caption.

Clade F: *asteroides* species group (Figs. 7 and 14)

27. The second and third ACA photophores are united in a common, isolated organ (Fig. 3C, E). One species in the *asteroides* group, *P. laternatus,* is polymorphic, usually having these photophores united. Individuals of *P. laternatus* with the second and third photophores isolated are uncommon.

In other species of *Polyipnus* (except *P. fraseri* which lacks ACA photophores) these light organs are not united. In some species (e.g., *P. kiwiensis*) they are so close to one another that they appear united; dissection is needed to reveal the lack of a connecting lumen. In *Argyropelecus,* ACA photophores are absent and in *Sternoptyx* there appears to be one. *Argyripnus* and *Sonoda* have numerous united photophores in a horizontal line that may be, in part (serially), homologous to ACA of *Polyipnus.* With the extreme dorsal displacement of ACA photophores in *Polyipnus,* however, it is not clear that united elements necessarily represent the plesiomorphic condition. It is more parsimonious to interpret the arrangement of these photophores in *Polyipnus* as derived.

28. The maxillary bone is densely pitted (e.g., *P. clarus* and *P. laternatus,* Fig. 10C, D, resp.). Slight pitting is present in *P. stereope, P. unispinus,* and the species of *Argyropelecus* and *Sternoptyx* but does not approach the condition in the *asteroides* species group.

Pitting of the maxilla is absent in all other *Polyipnus* species (e.g., *P. ruggeri* and *P. omphus,* Fig. 10A, B, resp.) and the species of the remaining sternoptychid genera.

29. The premaxilla is densely pitted in a manner similar to the maxilla (e.g., *P. clarus,* Fig. 10C).

In other *Polyipnus* species and the species of the remaining sternoptychid genera this bone is at most only slightly pitted (e.g., *P. ruggeri* and *P. omphus,* Fig. 10A, B, resp.).

30. The dorsal lamellar process of the maxilla, which is probably equivalent

to the palatinad facet of *Gonostoma* (Gonostomatidae) described by Stiassny (1986), is long, extending to the medial terminus of the bone near the midline (e.g., *P. clarus* and *P. laternatus,* Fig. 10C, D, resp.). A related modification is the heavy ossification of the maxilla with a lack of parallel ridges.

In other sternoptychid species this process, if present, is relatively short, not extending to the medical terminus of the maxilla (e.g., *P. ruggeri* and *P. omphus,* Fig. 10A, B).

31 (state 1). The dorsal bladelike process of the anterior ceratohyal has an arched or rounded profile (e.g., *P. laternatus* and *P. asteroides,* Fig. 9A, B, resp.).

In other *Polyipnus* species, and all those of *Sternoptyx* and *Argyropelecus* this process has a flattened profile (e.g., *P. soelae,* Fig. 9D). Other sternoptychid species lack such a blade.

Clade G: *bruuni* to *clarus* (Fig. 14)

32. The ventral process of the dentary symphysis is moderately elongate (e.g., *P. clarus* and *P. laternatus,* Fig. 10C, D, resp.).

This process is truncate in the *Polyipnus meteori* species group (e.g., *P. ruggeri,* Fig. 10A) and broadly triangular in the remaining *Polyipnus* species (e.g., *P. omphus,* Fig. 10B), and in all species of *Sternoptyx, Argyropelecus* and *Argyripnus.*

Clade H: *laternatus* to *clarus* (Fig. 14)

33 (c). A paired ventrally-directed external spine is present on the ventral surface of the first anal-fin proximal radial. Similar spines are also present in the *P. omphus* species group (e.g., *P. unispinus,* Fig. 12B), presumably through convergence. Paired spines are also present in *Sternoptyx* species but these are highly modified (Weitzman, 1974: 448, fig. 112) and probably convergent with those of the species of *Polyipnus.* If the spines in *Polyipnus* species are homologous with those of the species of *Sternoptyx,* then losses would be implied for *Argyropelecus* species, the *P. spinosus* group, *P. danae, P. meteori* species group, and at least *P. triphanos* of the *asteroides* group. Such an interpretation requires so many ad hoc arguments that it is rejected here.

Such spines are lacking in other *Polyipnus* species and the remaining sternoptychids.

34 (c). The infrapharyngobranchial of the second branchial arch has a long uncinate process (e.g., *P. clarus,* Fig. 13B). A somewhat similar condition exists in other sternoptychid species, especially those of *Argyropelecus, Argyripnus, Sonoda* and *Maurolicus* (Weitzman, 1974: 409, fig. 76). The form of this bone in clade H is therefore tentatively regarded convergent with the latter although on morphological grounds it appears primitive.

This bone is simple and rodlike or with a very short uncinate process in other *Polyipnus* species (e.g., *P. meteori,* Fig. 13A) and in species of *Sternoptyx.*

Clade I: *polli* to *clarus* (Fig. 14)

35. The primary longitudinal keel of the frontal has serrations restricted to the posterior half of its margin.

Other sternoptychids have this keel variously smooth or serrate over the entire margin.

36 (c). The lateral ridge of the anterior ramus of the preopercle has several broad serrations. This condition appears to be convergent with similar serrations in *P. unispinus* and the *P. spinosus* species group.

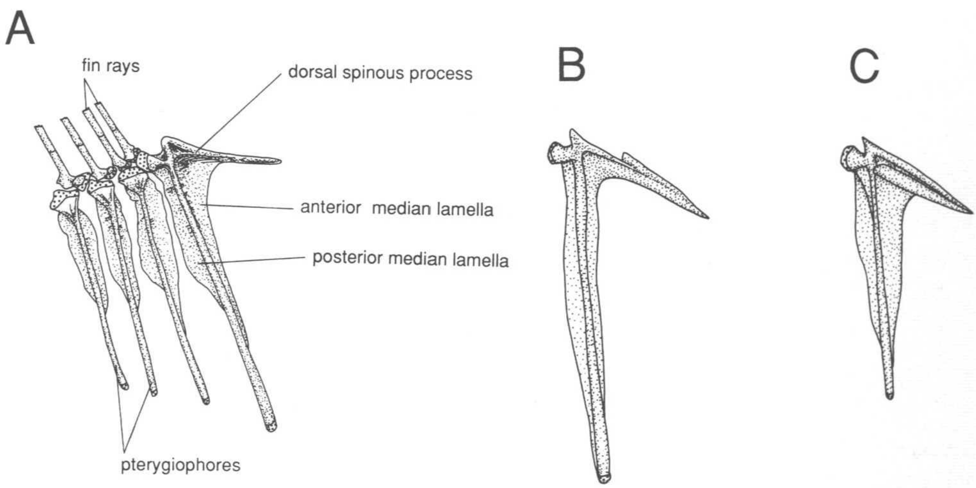

Figure 15. Dorsal fin pterygiophores, right side, laterval view: A, four anterior dorsal-fin pterygiophores, including anterior modified pterygiophore with dorsal spinous process, *Polyipnus clarus*, USNM 304745, 44.0 mm; B, anterior modified pterygiophore, *P. laternatus*, USNM 179050, 33.9 mm; C, anterior modified pterygiophore, *P. omphus*, ZMUC P206933, 48.0 mm.

All other *Polyipnus* species have no serrations in this position. Of the other sternoptychids only *Sternoptyx* species (variable among species) have serrate anterior preopercular rami.

37 (c). The shafts of the proximal radials posterior to the anal-fin hiatus are cylindrical. This character is convergent with similar radials in clade N (*P. danae* plus *P. unispinus*).

In all remaining *Polyipnus* species, species of *Argyripnus* and *Sonoda megalophthalma* (Weitzman, 1974: 417, fig. 82), the shafts are proximally expanded in the median plane. Cylindrical radial shafts, which likely represent the primitive condition within the Sternoptychidae, occur in species of *Argyropelecus, Sternoptyx* and *Maurolicus.* With respect to the phylogenetic reconstruction presented here, expanded radial shafts are regarded as primitive within *Polyipnus.*

Clade J: *asteroides, clarus* (Fig. 14)

38. The paired lateral lamellae of the dorsal spinous process extend only about one half of the distance from their posterior origins to the anterior margin of the anteromedian process (e.g., *P. clarus,* Fig. 15A, B, resp.).

All other *Polyipnus* species (e.g., *P. omphus,* Fig. 15C), except *P. fraseri* which lacks a dorsal spinous process, have these lamellae occupying the entire anterior-posterior axis of the pterygiophore. Outgroup comparisons outside *Polyipnus* are not possible since the somewhat similar "dorsal blades" of *Argyropelecus* and *Sternoptyx* are unpaired median structures made up of modified supraneurals.

Clade K: *omphus* + *spinosus* species groups (Fig. 7)

39. The posttemporal spine, or dorsal posttemporal spine in species with more than one spine, is very long (at least 10% SL) (e.g., *P. danae* and *P. inermis,* Figs. 38, 49, resp.). The spine of *P. laternatus* (Fig. 32) approaches this condition, especially resembling that of *P. omphus* (Fig. 40), but is probably convergent.

All other *Polyipnus* species have a short posttemporal spine, usually much less

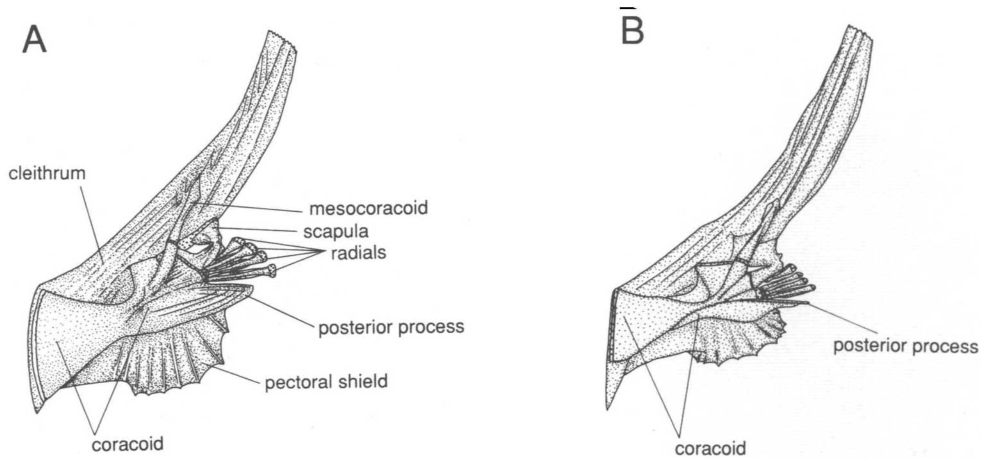

Figure 16. Ventral region of pectoral girdle, left side, medial view: A, *Polyipnus clarus*, USNM 304745, 44.0 mm; B, *P.* cf. *indicus*, USNM 316316, 38.0 mm.

than 10% SL (e.g., *P. meteori*, Figs. 8, 24). These spines are short, as in species of *Argyropelecus*, rudimentary in *Sternoptyx* species and lacking in the remaining sternoptychids.

40. The dorsal lamellar process (palatinad facet) of the maxilla is erect and tabular, its sides being nearly vertical (e.g., *P. omphus*, Fig. 10B).

This process has low relief with sloping sides in all other *Polyipnus* species (e.g., *P. ruggeri* and *P. clarus*, Fig. 10A, C, resp.), and species of *Argyropelecus*, *Sternoptyx* and *Argyripnus*.

41. The articular process of the coracoid for the attachment of the mesocoracoid is short (e.g., *P.* cf. *indicus*, Fig. 16B).

In all other *Polyipnus* species (e.g., *P. clarus*, Fig. 16A) and remaining sternoptychids this process is elongate, the point at which the two bones meet being dorsal to the surrounding surface of the coracoid.

31 (state 2). The dorsal winglike blade of the anterior ceratohyal has an angular anterodorsal surface (e.g., *P.* cf. *indicus* and *P. soelae*, Fig. 9C, D).

This blade is deep and rounded (derived in *asteroides* species group) (e.g., *P. laternatus* and *P. asteroides*, Fig. 9A, B) or very low in the *meteori* species group and species of *Argyropelecus* and *Sternoptyx* (Weitzman, 1974: 405, figs. 73, 74). Such blades do not occur in other sternoptychids.

43. The posteriorly-directed lateral process of the coracoid is narrow and terminates in an acute angle (e.g., *P.* cf. *indicus*, Fig. 16B).

This process is broad and its posterior termination rounded in other *Polyipnus* species (e.g., *P. clarus*, Fig. 16A) and either rounded or straight and vertical in other sternoptychids.

Clade L: *omphus* species group (Figs. 7 and 17)

44. The lateral lamellar processes of the dorsal spinous process are double, having secondary parallel ventrolateral elements (e.g., *P. omphus*, Fig. 15C).

Other *Polyipnus* species have a single pair of dorsolateral lamellae (e.g., *P. clarus* and *P. laternatus*, Fig. 15A, B, resp.). No other sternoptychid has such structures.

45. The ossified portions of the ectopterygoid and palatine bones do not overlap

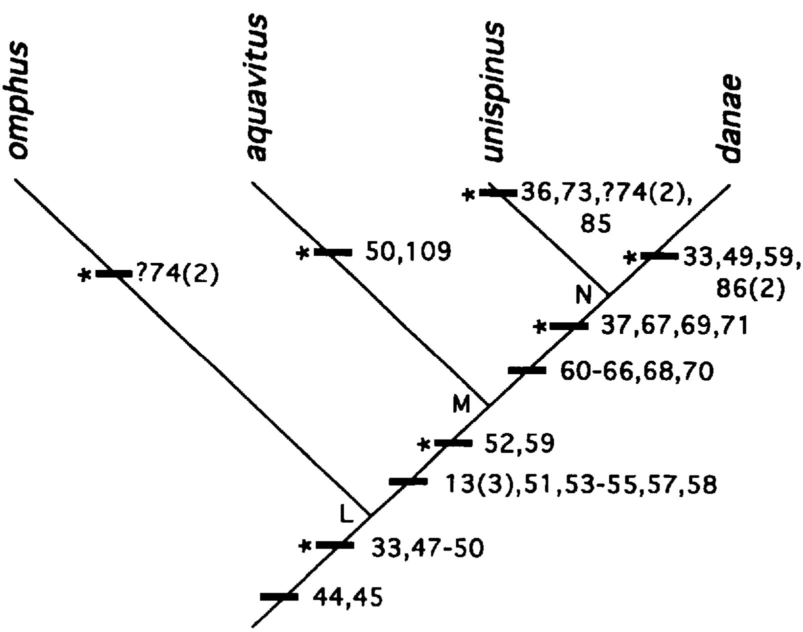

Figure 17. Cladogram depicting relationships of the *Polyipnus omphus* species group. Conventions defined in Figure 11 caption.

in lateral view. Contact of these bones occurs between the ossified dorsal termination of the ectopterygoid and the cartilaginous ventroposterior region of the palatine.

In other *Polyipnus* species (e.g., *P. meteori,* Fig. 8; *P. asteroides,* Weitzman, 1974: 356, fig. 30), and species of *Argyropelecus, Sternoptyx, Argyripnus* and *Sonoda* the ossified part of the palatine overlies the dorsoanterior extremity of the ectopterygoid.

33 (cr). Anal-fin pterygiophore spines are present (e.g., *P. unispinus,* Fig. 12B).

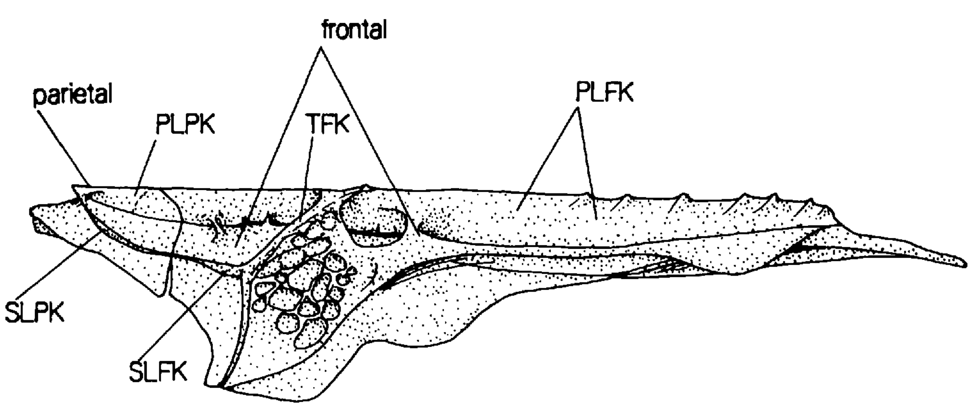

Figure 18. Frontal and parietal, right side, lateral view: *Polyipnus unispinus,* AMS I.19292-008, 28.0 mm. PLFK, primary longitudinal frontal keel; PLPK, primary longitudinal parietal keel; SLFK, secondary longitudinal frontal keel; SLPK, secondary longitudinal parietal keel; TFK, transverse frontal keel.

These spines are apparently independently derived with regard to those of the *P. asteroides* species group (*P. laternatus, P. asteroides, P. polli* and *P. clarus* only). Within the *P. omphus* species group the spines are lost in *P. danae.* Somewhat similar spines are also present in all species of *Sternoptyx* but they are highly modified in comparison to those of *Polyipnus* species. The homologies of these spines of the iliac process are not clear and the present assessment is made largely on the basis of parsimony.

Other sternoptychids lack such spines.

47 (cr). In adults there are 10 or more photophores in the ACB cluster (reversed in *P. fraseri* in which there are 4). This character is convergent with similar morphology in *P. laternatus* of clade H of the *asteroides* species group and in the species of clade U within the *P. spinosus* species group.

In other *Polyipnus* species, species of *Argyropelecus, Sternoptyx, Argyripnus* and *Sonoda paucilampa* Grey there are fewer than 10 ACB photophores. Other sternoptychids (e.g., *Valenciennellus* and *Danaphos* species) have at most three united photophores per individual ACB cluster.

48 (c). The dorsal step between ACB photophores #3 and #4 is indistinct (e.g., *P. omphus* and *P. unispinus,* Figs. 40, 41, resp.). Similar conditions in *P. laternatus* (Fig. 32) and clade U of the *P. spinosus* species group (e.g., *P. soelae,* Fig. 55) are interpreted as convergences. The polarization of this character is most parsimonious. Elevation of the posterior ACB photophores is correlated with proliferation of ACB number as described in character 47 above. It is possible that redundancy is introduced into the assessment of overall parsimony by considering the two characters independent. Evidence of independence is seen, however, in *P. fraseri* in which there are very few ACB photophores and no dorsal step between the third and fourth elements.

Other *Polyipnus* species have a distinct dorsal step between the third and fourth ACB photophores (e.g., *P. meteori, P. asteroides* and *P. asper,* Figs. 24, 27, 42, resp.). Comparisons to designated outgroups are ambiguous because of questionable homology of specific ACB photophores among ingroup and outgroup taxa.

49 (r). The paired anterolateral processes of the first anal-fin pterygiophore descend smoothly to the distal head (e.g., *P. unispinus,* Fig. 12B). This condition also occurs in *Sternoptyx* species but is convergent in the context of the cladogram. A reversed condition appears to be present in *P. danae* of this clade.

These structures are angular and dorsolaterally produced, to varying degrees, in the remaining *Polyipnus* species, and in all species of *Argyropelecus* (Weitzman, 1974: 419, fig. 84), *Argyripnus* and *Danaphos.*

50 (cRr). The first branchiostegal ray of the posterior ceratohyal is narrow. This character reverses in *P. aquavitus* where the branchiostegal ray is expanded and bladelike. *Polyipnus triphanos* (*P. asteroides* species group) also has a narrow branchiostegal ray in this position, and this is interpreted as a convergence in the context of the parsimonious reconstruction.

This branchiostegal ray is expanded and bladelike in other *Polyipnus* species, *Argyropelecus lychnus* species complex (sensu Harold, 1993), and all other sternoptychids examined.

Clade M: *aquavitus* to *danae* (Fig. 17)

51. The reflectors of the photophores of the ACC cluster (the ventral tubular portion covered by a modified platelike scale) are separated by very broad gaps, often greater than the diameter of one of these photophore reflectors (Fig. 4D; e.g., *P. aquavitus,* Fig. 36). In clade Y there is a similar condition (e.g., *P. soelae,*

Fig. 55) but the gaps are narrower and heavily ossified scales are associated with each organ. In terms of the cladogram these should be regarded as convergent. Outside *Polyipnus* one further possible instance of convergence occurs in the *Argyropelecus affinis* species complex (sensu Baird, 1971) (Weitzman, 1974: 336, fig. 11). In this case, however, the OV, VAV, and all AC photophores are widely spaced and in many cases remain separate from each other throughout ontogeny, likely a derived condition itself. The ACC photophores in *A. affinis* and *A. gigas* do not develop by budding from a common cluster as they do in *Polyipnus* species.

Photophore reflectors of the ACC cluster are compact (Fig. 4E) and frequently in contact with one another in other *Polyipnus* species (e.g., *P. meteori,* Fig. 24) and in the remaining sternoptychids that have a cluster in this position (*Sternoptyx* species, *Argyropelecus lychnus* species complex, and species of *Argyripnus, Sonoda, Danaphos, Valenciennellus, Maurolicus* and *Araiophos*).

52. The longitudinal keel of the parietal has a smooth margin (e.g., *P. unispinus,* Fig. 18). Although superficially a similar condition exists among species of *Argyripnus* the structure of the keel itself is different from that of *Polyipnus* and is rejected here as homologous on these grounds as well as parsimony. In view of miniaturization in clade M the lack of ornament here may be paedomorphic, resulting from truncation or retardation of development of ossified structures.

Such parietal keels are serrate to varying degrees in all other *Polyipnus* species, and species of *Argyropelecus* and *Sternoptyx.*

53. The paired perichondral ossifications on the distal radials of the anal-fin are small.

These plates are relatively large in all remaining *Polyipnus* species but absent in other sternoptychids. In *P. aquavitus, P. unispinus* and *P. danae* this character is most parsimoniously regarded apomorphic. The absence of these ossifications is clearly a synapomorphy of the Sternoptychidae, considering their presence throughout the other stomiiform families and nonstomiiform basal euteleosts. Their occurrence in *Polyipnus* is, therefore, atavistic in view of the well-corroborated derived position of the genus in the Sternoptychidae, as formulated by Weitzman (1974).

54. The distal radial cartilages of the anterior (excluding the first two) anal-fin pterygiophores are approximately equidimensional with a circular to triangular profile (e.g., *P. unispinus,* Fig. 12B).

Other *Polyipnus* species and the remaining sternoptychids examined have these radials elongate in the anterior-posterior axis and with an acute triangular profile (e.g., *P. meteori,* Fig. 12A).

55. The paired spines of the modified anterior dorsal-fin pterygiophore are long and needlelike.

Other *Polyipnus* species have much shorter, flattened spines. Uniqueness of the structure of this dorsal-fin pterygiophore of *Polyipnus* makes outgroup comparisons to other genera inappropriate.

13 (state 3). The ectopterygoid is very short, broad and anteriorly truncate.

The ectopterygoid is long and triangular in *P. omphus,* the *P. asteroides* species group (Weitzman, 1974: 356, fig. 30) and other sternoptychids (e.g., *Argyripnus atlanticus,* Weitzman, 1974: 354, fig. 27). Other forms of the ectopterygoid are independently derived for the *P. meteori* (clade C) and *P. spinosus* (clade O) species groups.

57. The dorsal preopercular spine is simple in structure but relatively large.

This spine is also elongate in *P. nuttingi* and *P. indicus* of the *P. spinosus* species group but does not approach the relative size that occurs in clade M.

Other *Polyipnus* species either lack this spine or it is very short with its length about equal to that of a preopercular serration. A dorsal preopercular spine is present, but modified, in species of *Argyropelecus*. These spines do not occur in other sternoptychids.

58. Small body size, not exceeding 40 mm SL. *Argyropelecus hemigymnus* appears to have independently undergone evolutionary size reduction (Harold, 1993).

All other *Polyipnus* species, and all species of *Sternoptyx, Argyripnus, Sonoda* and the remaining *Argyropelecus* species attain body sizes in excess of 40 mm.

59 (r). The anterior margin of the ascending limb of the parasphenoid extends anteriorly to the posterior extremity of the basisphenoid-parasphenoid articulation. In the context of the cladogram this character is reversed in *P. danae* to a condition resembling that of the outgroups.

In all other *Polyipnus* species (e.g., *P. meteori,* Fig. 8) and other sternoptychids, except *Argyropelecus* species in which the basisphenoid is lacking, the anterior margin of the ascending limb is posterior of the basisphenoid (e.g., *Argyripnus atlanticus* and *Sternoptyx diaphana,* Weitzman, 1974: 354, 359, figs. 27, 34, resp.).

Clade N: *danae, unispinus* (Fig. 17)

60. The caudal peduncle is very long and cylindrical or rodlike. This feature is unique to *P. danae* and *P. unispinus* (Figs. 38, 41, resp.). In many *Polyipnus* species there is some elongation but not approaching the extreme case in evidence here.

No other sternoptychid has a caudal peduncle with comparable shape.

61. The ventral process of the retroarticular is produced as a long spine.

This process is somewhat spinelike albeit very short in some other *Polyipnus* species (e.g., *P. aquavitus, P. inermis* and *P. indicus*). Remaining *Polyipnus* species (e.g., *P. asteroides,* Weitzman, 1974: 356, fig. 30) and other sternoptychids (e.g., species of *Argyripnus, Sonoda, Argyropelecus* and *Sternoptyx,* Weitzman, 1974: figs. 27, 28, 32, 34) have a rounded conical retroarticular process.

62. The median lamellae on the shafts of the anal-fin proximal radials (excluding the first pterygiophore) are restricted to the distal one half of the bone and are somewhat teardrop-shaped overall in lateral view (e.g., *P. unispinus,* Fig. 12B).

In other *Polyipnus* species (e.g., *P. meteori,* Fig. 12A), and species of *Argyropelecus, Sternoptyx* and *Argyripnus* these lamellae extend at least to the vicinity of the proximal tip of the bone (e.g., *Argyropelecus aculeatus,* Weitzman, 1974: 419, fig. 84).

63. The shaft of the anterior dorsal-fin pterygiophore inserts fewer than six vertebrae anterior of the first anal-fin pterygiophore. The only other sternoptychid examined with this feature was *Argyripnus* sp. from the Philippines.

In all other *Polyipnus* species, species of *Argyropelecus* and *Sternoptyx,* and *Argyripnus atlanticus* the first dorsal-fin pterygiophore inserts at least six vertebrae anterior to the anal fin origin.

64 and 65. The external spinous processes of the first dorsal-fin pterygiophore (64) and its shaft (65) are greatly enlarged. These features are treated as separate characters since they undergo independent variation within and between species of deep-bodied sternoptychids.

In other *Polyipnus* species the dorsal spinous process is relatively small and the shaft is similar in length and diameter to the second pterygiophore.

66. The perichondral ossifications of the dorsal-fin distal radials are very small. These plates are relatively large in other *Polyipnus* species but absent in other sternoptychid genera.

67 (c). The secondary longitudinal keel of the frontal is discontinuous, its margin descending to the surface of the surrounding bone (e.g., *P. unispinus,* Fig. 18).

This keel is continuous in all other *Polyipnus* species, except *P. nuttingi* in which it is lacking. In *Argyripnus* species there is a continuous keel but its structure is somewhat unusual and is probably not homologous with that of *Polyipnus* species. Other sternoptychids lack this keel.

68. The ossified dorsal and ventral hypohyals are very small and separated by a broad field of cartilage.

In the remaining species of *Polyipnus* (Fig. 9) and species of the other sternoptychid genera the dorsal and ventral hypohyal ossifications are large, approaching or even contacting one another.

69 (c). The longitudinal lamellae of the pectoral fin radials are highly reduced. A similar condition occurs in *P. polli,* probably as a convergence.

Such lamellae are well-developed in all other *Polyipnus* species and species of *Argyropelecus* and *Argyripnus* but altogether lacking in species of *Sternoptyx.* In terms of parsimony, members of the latter genus lack these structures as a convergence rather than primitive absence.

70. The fifth ceratobranchial has long, sparse teeth in a patch at the proximal end of the bone.

Long, sparse teeth are present in other *Polyipnus* species (except the *P. spinosus* species group), and species of *Argyropelecus, Sternoptyx* and *Argyripnus* but they are distributed along most of the proximal half of the bone. In the *Polyipnus spinosus* species group the tooth patch occupies the proximal one half of the ceratobranchial but the teeth themselves are very short and densely packed.

71 (c). There are no lateral tooth plates associated with the fifth ceratobranchial. This is also true of *P. triphanos* and *Sternoptyx* species, conditions which are here interpreted parsimoniously as convergent.

These tooth plates are present in all other *Polyipnus* species, and species of *Argyropelecus, Argyripnus* and *Sonoda* (Weitzman, 1974: 410, fig. 77).

Clade O: *spinosus* species group (Figs. 7 and 19)

72. The ventral preopercular spine is ventrally-directed, very long and scythe-like, with some degree of anterior arc (Fig. 6A).

Other *Polyipnus* species have either a reduced spine (*asteroides* and *meteori* species groups, not including *P. laternatus*) or a short relatively weak conical spine (*P. omphus* species group and *P. laternatus*). These spines are of moderate length in *Argyropelecus* and *Sternoptyx* species but do not approach the size and configuration of those of the *spinosus* species group. Preopercular spines do not occur in other stomiiforms.

73 (c). The ventral margins of the platelike scales covering the PV photophores have strong denticles, similar to fused cteni in the terminology of Roberts (1993), which extend distally from prominent "radii" (Fig. 4A, C). These "radii" are parsimoniously interpreted as being not homologous to those of the scales of the other teleosts since their occurrence among stomiiforms is restricted to *Polyipnus*

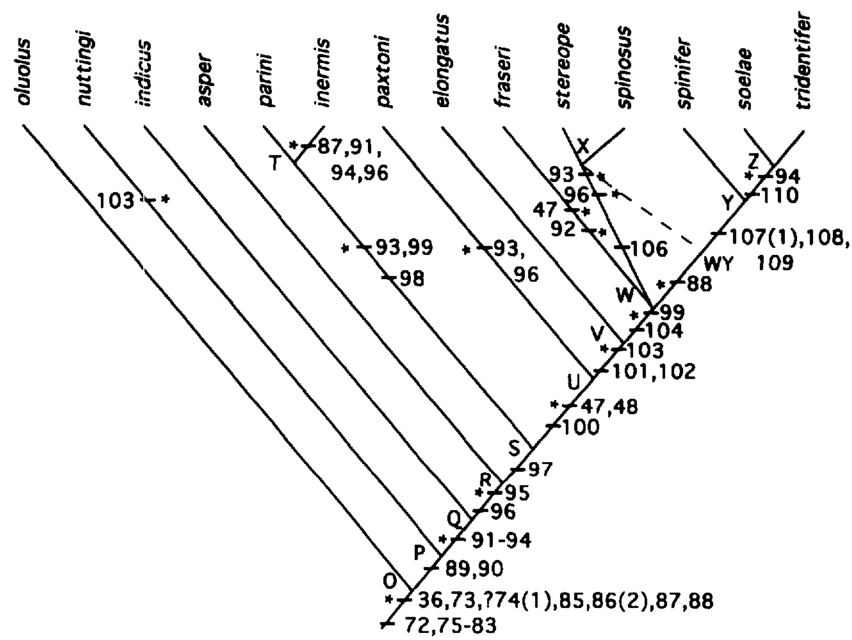

Figure 19. Cladogram depicting relationships of the *Polyipnus spinosus* species group. Conventions defined in Figure 11 caption.

and *Argyropelecus*, members of a terminal clade. Material examined for this study indicates that stomiiform fishes have true scales but they lack radii.

In *P. inermis* PV scale denticles are present but weak as in other photophore clusters of that species. Outside the *P. spinosus* species group PV scale denticles are present in *P. unispinus* (*P. omphus* species group) but in the latter species the denticles are minute and lack radii; apart from these morphological differences a consideration of parsimony indicates that the structures in these two cases are not homologous. In *Argyropelecus sladeni* there are PV scale denticles in some individuals from the Pacific Ocean. This trait may also have arisen independently.

All other members of *Polyipnus* and *Argyropelecus* lack PV scale denticles (Fig. 4B), as is the case for all other stomiiforms.

74 (c). The ventral margin of the dentary is deeply serrate. *Polyipnus omphus* and *P. unispinus* (*P. omphus* species group) also have serrations but these are minute scallops and may not be comparable to those of the *spinosus* species group. If these features were treated as homologues there would be two equally parsimonious solutions: (a) independent derivation in the *spinosus* group, *P. omphus* and *P. unispinus*, and (b) a synapomorphy of clade K with inferred losses in *P. aquavitus* and *P. danae*. There would be no effect on the cladogram topology.

All other *Polyipnus* species and the remaining sternoptychids have dentaries with a smooth ventral margin.

75. The lateral surface of the ventral limb of the posttemporal, which is fused with the supracleithrum (Weitzman, 1974), is serrate.

In other sternoptychids, regardless of whether the supracleithrum is fused with the posttemporal (remaining *Polyipnus* species and all species of *Argyropelecus*) or is a separate element, the ventral limb is smooth and without any serrations.

76. The posterior process of the posttemporal bone has more than one spine.

These spines have rodlike bases originating at and radiating from the posterior process. They are unlike associated serrations which are restricted to ridges and flangelike margins of the bone (Harold, 1989: 873, fig. 2) (Fig. 5A, B).

All other *Polyipnus* species (Fig. 5C), and all species of *Argyropelecus* and *Sternoptyx* have to various degrees of development single posttemporal spines. Other sternoptychids lack posttemporal spines.

77. The shaft of the first proximal radial of the dorsal fin does not have an anterior median lamella.

Such lamellae are present in all other *Polyipnus* species (e.g., *P. clarus*, Fig. 15A), and the species of *Argyropelecus, Sternoptyx, Argyripnus* and *Maurolicus*.

13 (state 1). The ectopterygoid is elongate and very narrow. This condition is one of three forms of ectopterygoid in *Polyipnus* which, according to this phylogenetic reconstruction, are possibly independently derived.

The ectopterygoid is broad and triangular throughout the *asteroides* species group, *P. omphus*, and in the species of *Argyropelecus, Sternoptyx, Argyripnus* and, according to Weitzman (1974), *Sonoda megalophthalma*.

79. The ectopterygoid has a median ridge or keel which describes a broad arc.

This ridge is deflected through an acute angle dorsally in the remaining *Polyipnus* species, and species of *Argyropelecus, Sternoptyx* and *Argyripnus*.

80. The frontal bone has a lateral secondary longitudinal keel which does not extend posteriorly to the secondary parietal keel.

In all other *Polyipnus* species (e.g., *P. unispinus*, Fig. 18) and in *Argyripnus* species such a frontal keel extends posteriorly and is continuous with the secondary parietal keel. These keels do not appear to occur in other sternoptychids.

81. The posterior shelf of the epioccipital is modified into a cuplike socket at which the dorsal limb of the posttemporal articulates.

Other sternoptychids lack such modification of the epioccipital.

82. Along the proximal one half of the ceratobranchial of the fifth gill arch there is a medial patch of densely packed short teeth, corresponding to the fused tooth plate.

Other sternoptychids have sparse, long teeth on this bone.

83. The dorsal limb of the posttemporal bone has deep spinelike serrations (Fig. 5A). Outside the *spinosus* species group weak serrations are present in the *meteori* species group. However, the ridges on which these serrations originate differ in their structure, tending to support a hypothesis of independent derivation.

Such serrations are absent in all other sternoptychids.

36 (state 1) and 85 (c). The anterior (36) and the dorsal (85) rami of the preopercle have deep spinelike serrations. The anterior ramus has several weak serrations in *P. unispinus, P. polli, P. asteroides, P. clarus* and some *Sternoptyx* species. Weak serrations of the dorsal ramus occur in *P. unispinus*, and species of *Argyropelecus* and *Sternoptyx*. It is likely that the deep serrations seen in members of the *spinosus* species group represent an apomorphic condition.

These serrations are absent in all other *Polyipnus* species and the remaining sternoptychids.

86 (c) (state 2). The antorbital is a minute transversely elongate element. A somewhat similar ossification also occurs in *P. danae* but was not observed in other members of the *P. omphus* species group. It is quite possible bones of such delicate structure and superficial position could be easily lost during capture through net rolling.

The antorbital is well-developed and equidimensional to dorsoventrally elongate in *P. omphus, P. meteori* species group, and the species of *Argyripnus*,

Danaphos and *Maurolicus* but absent in the *P. asteroides* species group, *P. unispinus, P. aquavitus,* and species of *Sternoptyx* and *Argyropelecus.*

87 (r). The anterodorsal surface of the dorsal spinous process is to varying degrees serrate. *Polyipnus inermis* is the only member of the *spinosus* group lacking these serrations, except *P. fraseri* which lacks any extension of the first dorsal pterygiophore beyond the body surface; this is clearly a secondary absence considering the otherwise ubiquity of the structure in the genus.

All other *Polyipnus* species have a nonserrate dorsal spinous process. "Dorsal blades" in all species of *Argyropelecus* and *Sternoptyx* are usually serrate but, as discussed, they are not structurally comparable to those in *Polyipnus.* In *Polyipnus* the presence of serrations is parsimoniously interpreted as derived.

88 (r). An absence of palatine teeth is probably derived for clade O but reverses to presence at a lower level of generality (clade WY).

Other sternoptychids have palatine teeth.

Clade P: *nuttingi* to *tridentifer* (Fig. 19)

89. The third ACA photophore is united with the anterior ACB photophore, forming a continuous organ (Fig. 3A; e.g., *P. indicus,* Fig. 48).

In all other *Polyipnus* species the third ACA photophore is not joined to the first ACB element (Fig. 3B–E). A single ACA is present in the species of *Sternoptyx* and is not joined with the ACB cluster but as already mentioned there is some doubt about homology of this photophore. The VAV/ACA photophores of *Argyripnus* and *Sonoda* species are separated from the ACB by a broad gap.

90. The scales of the VAV photophores are denticulate. These structures are present but very weak in *P. inermis* which has various reductions of scale denticles and spinous processes. The occurrence of similar structures in *Argyropelecus aculeatus,* a member of the terminal clade of that genus (Harold, 1993), is viewed as a likely convergence.

Other sternoptychids with VAV scales, i.e., all other species of *Polyipnus* and most *Argyropelecus,* do not have denticles.

Clade Q: *indicus* to *tridentifer* (Fig. 19)

There are four derived characters in support of clade Q none of which is unique to all members of the group.

91 (r). The ventral margin of the angular is minutely serrate in all clade Q species except *P. intermis.*

Other sternoptychids have a smooth angular.

92 (r). The point of insertion on the maxilla for the posterior limb of the premaxilla is angular to deeply incised. This character is reversed in *P. fraseri* which has a rounded insertion point.

In other *Polyipnus* species, and all species of *Agyropelecus, Sternoptyx* and *Argyripnus* this insertion point is rounded or with a shallow concave incision. There is considerable intraspecific variation in the outgroups but deep sculpting as described above is restricted to clade Q.

93 (r). The scales of the ACC photophores are denticulate. This character is parsimoniously interpreted as being lost in clade T (*P. inermis* plus *P. parini*), *P. elongatus* and clade X (*P. stereope* plus *P. spinosus*). Similar denticles also occur in *Argyropelecus aculeatus* and sporadically in *A. sladeni* populations from the Pacific Ocean.

Other sternoptychids lack denticulate ACC photophore scales.

94 (r). The lateral ridge of the dentary is serrate. This character reverses to nonserrate in *P. inermis* and clade Z (*P. soelae* plus *P. tridentifer*).

Other sternoptychids lack these serrations.

Clade R: *asper* to *tridentifer* (Fig. 19)

95. The posteriormost region of the primary keel of the parietal is modified into two minute, opposed spines (PKS in Fig. 6D), directed anteriorly and posteriorly. Based on the presence of this character, *Polyipnus* sp. B is a member of clade R.

This keel in other *Polyipnus* species is continuous (e.g., *P. unispinus*, Fig. 18) or with a central hiatus, and in *Sternoptyx, Argyropelecus* and *Argyripnus* species it is continuous.

96 (r). Denticles are present on ACB scales. Although this character is interpreted as derived for clade R there are three instances of putative loss: *P. inermis, P. elongatus,* and clade X (*P. stereope* plus *P. spinosus*).

Other sternoptychids lack denticulate ACB photophore scales.

Clade S: *inermis* to *tridentifer* (Fig. 19)

97. Three spines originate on the posterior process of the posttemporal bone (Fig. 5A). Although the median and ventral spines are in some species very short and indistinct there are always three spines.

In the remaining members of the *P. spinosus* species group there are two spines (Fig. 5B) although in some cases (e.g., *P. nuttingi*) there are many deep spinelike serrations on the posterior process of the posttemporal. Single posttemporal spines characterize the remaining *Polyipnus* species, and all species of *Argyropelecus* and *Sternoptyx.*

Clade T: *inermis, parini* (Fig. 19)

98. A broad gap, about equal to the diameter of one photophore reflector, is present between the reflectors of the third and fourth photophores of the ACB cluster (e.g., *P. inermis,* Fig. 49).

Disjunction of the ACB photophores is unknown in other sternoptychids with clearly equivalent light organs (i.e., remaining *Polyipnus* species, and all species of *Argyropelecus, Argyripnus* and *Sonoda*). In *Sternoptyx* species there are only three ACB photophores.

99 (c). In species with three posttemporal spines the ventral element is very long, at least one half of the length of the dorsal spine. This condition occurs possibly as a convergence in clade W (*P. fraseri* to *P. tridentifer*). Alternatively the long ventral spine is derived lower in the tree (clade S) and independently reduced in *P. paxtoni* and *P. elongatus.* However, the latter hypothesis requires an additional step and on the basis of parsimony is not preferred.

In other *Polyipnus* species with multispinose posttemporals the ventral/basal spine is short and resembles very closely those of *P. paxtoni* and *P. elongatus.*

93 (R). The ACC photophore scales are not denticulate. See clade Q (*P. indicus* to *P. tridentifer*) derived characters for comments.

Clade U: *paxtoni* to *tridentifer* (Fig. 19)

100. The articular heads of the posterior two dorsal-fin proximal radials are fused.

In other sternoptychids these radials are separate elements.

47 (cr). Ten or more united photophores are present in the ACB cluster. In *P. fraseri* there are only 4 ACB photophores, a condition which is parsimoniously interpreted as being a derived character and paedomorphic (Harold, 1990b). In addition, proliferation of these photophores occurs in *P. laternatus* and in the *P. omphus* species group as convergences in the context of the cladogram. All of the species of two outgroup genera, *Maurolicus* and *Sonoda* (but not its sister group *Argyripnus*), also have relatively high ACB counts that, in terms of parsimony, represent secondary derivations.

Other sternoptychids have fewer than 10 ACB photophores.

48 (c). The dorsal step between the third and fourth ACB photophores is not pronounced (e.g., *P. paxtoni*, Fig. 54). This apparently reductive character also occurs in *P. laternatus* and the *P. omphus* species group as convergences.

Other *Polyipnus* species have a pronounced step (e.g., *P. meteori*, Fig. 24), an unusual condition among stomiiforms but probably not synapomorphous in view of the number of conflicting derived characters. This kind of photophore arrangement should be regarded as derived at the level of the genus *Polyipnus*.

Clade V: *elongatus* to *tridentifer* (Fig. 19)

101. The anterior angle of the pectoral shield is deflected laterally as a spinous process.

Other sternoptychids with a pectoral shield (remaining *Polyipnus* species and all species of *Argyropelecus*) do not have laterally-deflected processes.

102. The bladelike process on the dorsal surface of the anterior ceratohyal is low and restricted to the anterior region of the bone. This process has a concave anterior margin for reception of the dorsal hypohyal (e.g., *P. soelae*, Fig. 9D).

The plesiomorphic condition, a low rounded process without anterior concavity, occurs in other *Polyipnus* species except the *asteroides* and *meteori* species groups as well as the species of *Sternoptyx* and *Argyropelecus*. Such processes are lacking in other sternoptychids.

103 (c). The lateral surface of the parhypural is minutely spinose. A somewhat similar but, according to parsimony, likely independently derived condition occurs in *P. nuttingi* and in the *Argyropelecus lychnus* species complex.

Other sternoptychids lack parhypural spines.

Clade W: *fraseri* to *tridentifer* (Fig. 19)

104. The ventral posttemporal spine is slightly curved towards the anterior (Fig. 5A).

In other *Polyipnus* species with multispinose posttemporals this spine is essentially straight or with slight dorsal curvature. Other sternoptychids lack ventral posttemporal spines.

99 (c). In *Polyipnus* species with three posttemporal spines the ventral element is very long, at least one half of the length of the dorsal spine (Fig. 5A). A similar condition occurs in clade T (*P. inermis, P. parini*) which should be considered convergent in the context of the cladogram.

Clade WY: *stereope* to *tridentifer* (Fig. 19)

There are no ubiquitous unreversed synapomorphies at this level and therefore node WY "collapses" into an unresolved trichotomy at node W.

88 (R1). Teeth are present on the palatine bone. Some specimens of *P. tridentifer* lack these teeth but McCulloch (1914: 87) noted the presence of one or two small teeth on the anterior end of the palatine in the type series.

Most sternoptychids, and virtually all other stomiiforms examined, have palatine teeth: their loss appears to be derived at the level of clade O (''base'' of the *spinosus* species group) thus yielding the absence of such teeth as plesiomorphic within the group.

Clade X: *stereope, spinosus* (Fig. 19)

106. The caudal peduncle is very deep and stout, with a slight posterior taper (Figs. 57, 59). The caudal peduncle of *Polyipnus omphus* also has a slight posterior taper (Fig. 40) but is much shallower and overall the shape does not compare well with that of *stereope* and *spinosus.*

All remaining *Polyipnus* species and other sternoptychids have variously elongate caudal peduncles with dorsal and ventral surfaces essentially parallel (e.g., *P. tridentifer,* Fig. 60).

93 (cR) and 96 (cR). The scales of the ACC and ACB photophores do not have denticles. See clade T (*P. inermis, P. parini*) derived characters for further comments.

Clade Y: *spinifer* to *tridentifer* (Fig. 19)

107. The predorsal pigment notch is indistinct, appearing only as a very slight inflection of the ventral margin of the dorsum pigment (Figs. 55, 56, 60).

All other *Polyipnus* species have to varying degrees a raised area in this position (e.g., *P. inermis,* Fig. 49) except *P. unispinus* which has an essentially straight pigment margin along the entire length of the body (Fig. 41). A raised area of the pigment margin occurs in species of *Argyropelecus* suggesting that this pattern of pigmentation is likely plesiomorphic within *Polyipnus.*

108. The reflectors of the ACC photophores are separated by spaces which are less than or equal in width to the diameter of one photophore. A similar dispersion of the ACC photophores occurs in the miniature species *P. aquavitus, P. unispinus* and *P. danae* of the *P. omphus* species group which, in terms of parsimony, is convergent with the clade Y arrangement. Additionally, in the *Argyropelecus affinis* complex, a general spreading apart of OV, VAV and AC photophores occurs but the mechanism by which this arrangement is attained is different from *Polyipnus* species.

In other sternoptychids with comparable ACC clusters (remaining *Polyipnus* species, and the species of *Argyropelecus, Sternoptyx, Argyripnus, Sonoda, Danaphos, Valenciennellus* and *Maurolicus*) these photophores are either in contact with one another or in close proximity.

109 (cR). The two epurals are separate basally but distally fused. One distantly-related species, *P. aquavitus,* has similar epural fusion. The distribution of epural fusion in the genus is odd and suspect as an indicator of relationship. *Polyipnus nuttingi, P. inermis, P. indicus, P. asper, P. paxtoni, P. elongatus* and *P. stereope* (members of the *spinosus* species group), and *P. unispinus,* (*omphus* species group) have completely fused epurals while in all remaining species (e.g., *P. meteori,* Fig. 24) for which cleared and stained preparations were available the epurals are separate.

Complete fusion of the epurals appears to be plesiomorphic within the *P. spinosus* species group yielding the partial fusion in clade Y as a derived condition.

In other sternoptychids the epural is a single or fused ossification as in *Argyropelecus* and *Sternoptyx* species or single and cartilaginous as in *Sonoda* species (Weitzman, 1974: 427, fig. 93) and *Maurolicus* sp.

Clade Z: *soelae, tridentifer* (Fig. 19)

110. The ventral margins of the anterior ACB photophore scales have at most a single denticle. The parsimonious interpretation of this character indicates that the presence of a single denticle is a derived albeit reductive feature.

Other *Polyipnus* species have either numerous or no ACB scale denticles. These denticles are lacking in other sternoptychid genera.

94 (cR). The lateral ridge of the dentary is smooth and not serrated.

Other members of the *P. spinosus* species group except *P. inermis* have serrations. No other sternoptychid has this ridge serrated. It is most parsimonious to view these similarities in dentary ornamentation as being convergent.

MONOPHYLY AND RELATIONSHIPS OF *POLYIPNUS*

Weitzman (1974), in a study of the intergeneric relationships of sternoptychid fishes, listed features that were thought unique to *Polyipnus.* He examined only four species but the characters appear to be valid synapomorphies on the basis of the present expanded set of taxa: a) shelflike posterior processes of the epioccipital (character 1, this study), b) relatively short anterior ceratohyal (character 2), c) large dorsoventrally expanded urohyal (character 3), d) reduction of the centrum-like facet of the basioccipital, e) large sagitta, much deeper than long, f) club-shaped cartilaginous and bony palatine, g) unique long upper jaw ligaments coupled with very long ascending process of the premaxillary, h) arrangement and configuration of the supraethmoid, lateral ethmoids and vomer associated with a highly modified arrangement of the ethmoid region and i) short dentary with a relatively deep middle area. In the present study preservation of sagittae has precluded an adequate appraisal of e) above. Length of the ascending process of the premaxillary as described in g) above actually varies within *Polyipnus.* Elongation of the ascending process which is also characteristic of *Argyropelecus* appears to be plesiomorphic within *Polyipnus.* The broad triangular form of the premaxillary ascending process of the *P. meteori* species group (clade C, character 15) is, therefore, apomorphic. The unusually long upper jaw ligaments mentioned are derived for *Polyipnus* and related to the novel jaw protrusability. The remaining characters listed above were corroborated by observations of some species but were not encoded for the study of species interrelationships.

Among new characters in support of monophyly of *Polyipnus* is the presence of a steplike increase in elevation of the fourth relative to the third ACB photophore. While being inconspicuous in about half of the species (e.g., *P. paxtoni*), the feature is present in all forms except *P. fraseri.* In the latter these photophores are considerably reduced in size and the step may as a result be obscured. Another possibility is that the four ACB photophores in *P. fraseri* are actually equivalent to the third ACA followed by the first three ACB photophores as they occur in the other species. In either case, since the development of this photophore cluster in *P. fraseri* has likely been modified through some heterochronic process (Harold, 1990b), the steplike feature that was likely present in the common ancestor of clade W has probably also been affected.

The disrupted configuration of the three OVB photophores appears to be unique in *Polyipnus.* Within the genus there are several arrangements that in some cases define clades, but common to all is the dorsal displacement of at least one of the three OVB elements. Occurrence of three ACA photophores (character 4) is considered synapomorphic of *Polyipnus,* though lacking in *P. fraseri* (heterochronic reduction).

The L or lateral photophore is positionally unique and should be considered

synapomorphous. Weitzman (1974: 461, table 1) considered the L photophore synonymous with anterior VAL in other stomiatoids (=stomiiforms). This seems reasonable inasfar as the L is located slightly posterior of a vertical line through the base of the pelvic fin. However, absence of VAL in the outgroups decreases the likelihood of homology.

The presence of a bilateral dorsal spinous process (character 6), a modification of the anteriormost dorsal fin pterygiophore possibly involving one or more supraneurals is a *Polyipnus* synapomorphy. As a further reductive character, the process is lacking in *P. fraseri* or at least is not external or visible in x-radiographs. This and other unique reductive characters in this species are inferred to be autapomorphies based on the well-corroborated placement of *P. fraseri* in the *spinosus* group.

Another putative synapomorphy of *Polyipnus* is the presence of paired perichondral ossifications associated with the distal radials of the anal and dorsal fins. These ossifications do not occur in other sternoptychid genera (Weitzman, 1974) but are widespread in other stomiiform families (Weitzman, 1974; Fink and Weitzman, 1982; Fink, 1985). In view of Weitzman's (1974) well-corroborated phylogeny of the Sternoptychidae it is unlikely that these structures in *Polyipnus* on the one hand and the remaining stomiiforms on the other, are homologues.

Seven rather similar species were referred to the *asteroides* species complex by Baird (1971), but not based on a phylogenetic analysis. These species comprise much of clade B (*meteori* plus *asteroides* species groups). I add to this group *P. ovatus, P. bruuni* and *P. clarus,* which are new species, and *P. laternatus* is moved from another previously recognized group, the *laternatus* complex (Baird, 1971). Because the relationships of *P. laternatus* are somewhat contentious, the evidence in support of its placement in the *asteroides* group is discussed here in some detail. This species was thought by Baird on the basis of body shape and size, posttemporal spine length, photophore configuration, and dentition to be most closely related to *P. omphus, P. unispinus,* and *P. aquavitus.* Of these characters, body shape and size do not differ significantly between the two groups. *Polyipnus laternatus* is a relatively stout-bodied species that reaches sizes comparable to *P. omphus* and members of the *meteori* and *asteroides* species groups. Concerning dentition, the arrangement in *P. laternatus* is plesiomorphic and resembles that of both groups. The posttemporal spine is slightly longer than in other clade B species but does not reach 10% SL as it does in the *P. omphus* species group. This character and the large number (up to 13) of ACB photophores appear to be convergent in the context of the most parsimonious hypothesis of relationships. Contrary to Baird's conclusions, one aspect of photophore configuration, the dorsal displacement of the second and third ACA photophores, supports the hypothesis that *P. laternatus* is more closely related to members of the *meteori* and *asteroides* species groups (together clade B) than to the *omphus* and *spinosus* species groups (clade K).

Monophyly of clade B is also supported by the presence of an expanded urohyal with a convex, rounded posterior margin (character 7) and the "V" configuration of the OVB photophores (character 11). The presence of a reduced ventral preopercular spine (character 10) unites all of these species except *P. laternatus* which has a short but well-developed spine. The upper jaw in the *asteroides* group has undergone a number of modifications which unite its members. Among these are the dense pitting of the maxilla and premaxilla (characters 28 and 29), and the medial extension of the palatined facet to the midline (character 30). The rounded bladelike process of the anterior ceratohyal (character 31[1]) and the uniting of the second and third ACA photophores in a common organ (character

27) are additional synapomorphies of clade B (*asteroides* plus *meteori* species groups). *Polyipnus laternatus* is homoplastic in only one of these characters, preopercular spine structure; the species placement in the *asteroides* group is well-supported.

Within the asteroides group, *P. bruuni* is proposed as the sister group to *P. asteroides, P. clarus, P. polli,* and *P. laternatus* based on the shared unique elongate ventral process of the dentary symphysis (character 32). The position of *P. laternatus* as sister group to all other Atlantic *Polyipnus* (*P. asteroides, P. clarus,* and *P. polli*) is indicated by two homoplastic characters. One of these, the presence of anal-fin pterygiophore spines (character 33) also occurs in the Indo-Pacific *omphus* species group (lacking in *P. danae*). The other character (34), presence of a long uncinate process on the dorsal surface of the second infrapharyngobranchial, occurs in all outgroup genera except *Sternoptyx*. Based on all available evidence the uncinate process must be secondarily derived in *Polyipnus*.

Polyipnus laternatus lacks the proposed synapomorphies uniting the *omphus* species group (Baird's *laternatus* complex minus *laternatus*) with the *spinosus* group. In this large clade (clade K), the structure of the dorsal lamellar process or palatinad facet of the maxilla (character 40) is unique, being an erect, anteriorly concave structure. The structure in *P. laternatus* is clearly like that of other *asteroides* group members with low relief and gently sloping anterior and posterior surfaces. This is also the generalized condition seen in the outgroups. Other characters uniting the *omphus* and *spinosus* groups to the exclusion of *P. laternatus* are: a short coracoid process for articulation of the mesocoracoid (character 41), the posterior process of the coracoid terminating posteriorly in an acute angle (character 43), and the dorsal winglike blade of the anterior ceratohyal having an angular anterodorsal margin proximal to the hypohyals (character 31[2]). A serrate ventral dentary margin (character 74) may also be derived for the clade.

Baird (1971) initially recognized a morphological grouping of species roughly corresponding to the *meteori* species group. He treated *P. kiwiensis, P. matsubarai, P. meteori* plus *P. ruggeri* as a subgroup within his *asteroides* species complex, characterized by dentition of the posterior median process of the vomer and a unique configuration of SAN (=ACA) photophores. The *meteori* species group (clade C) is clearly monophyletic. In addition to derived vomerine dentition (character 12) the relationship is supported by unique ectopterygoid shape (character 13), reduction of the dorsal lamellar processes of the symplectic (character 14), a broadly triangular premaxillary ascending process (character 15), reduction of the diagonal ridge in the preopercular angle (character 16), truncation of the dentary symphyseal process (character 17), a short iliac spine (character 18) and fine serration of the dorsal limb of the posttemporal (character 19). The ACA photophore configuration mentioned by Baird (1971) is distinctive but not derived at this level.

According to Baird (1971), the species here referred to the *asteroides* species group (in its original form consisting only of *P. asteroides, P. polli* and *P. triphanos*) formed a "dichotomy" with the *meteori* species group. He did not discuss relationships in detail, indicating the differences between the two groups in an artificial dichotomous key. The unifying characters of the *asteroides-polli-triphanos* trio given by Baird are absence of teeth on the posterior process of the vomer, dorsal displacement of the second supra-anal (=ACA) photophore to the level of the third or higher, and a "nonsymmetrical" arrangement of supra-abdominal (=OVB) photophores. The vomerine dentition character is plesiomorphic and not a useful indicator of relationship. Dorsal displacement of the second ACA photophore is here considered a synapomorphy (character 8) of clade B (all spe-

cies here ascribed to the *meteori* and *asteroides* groups). Symmetry of OVB configuration exhibits too much intraspecific variation to be of any use at this level.

A phylogenetic relationship has not previously been proposed for the members of the *omphus* and *spinosus* species groups (i.e., clade K). Baird (1971) suggested that the species here referred to the *P. omphus* species group ("*P. laternatus* species complex," including *P. laternatus* but not *P. danae*) were most closely related to the *P. asteroides* species complex on the basis of "similar otoliths" and unspecified osteological resemblances. He further stated that the *P. spinosus* complex appeared primitive with regard to axial and caudal osteology.

Clade K is an assemblage of 18 species exhibiting a broad array of forms ranging from miniature, weakly ornamented species (e.g., *P. danae*) to relatively large, spinose forms (e.g., *P. tridentifer*). This apparently heterogeneous group is united by the following shared derived characters: a) extreme elongation of the (dorsal) posttemporal spine (at least 10% SL) (character 39), b) a tabular process on the dorsomedial surface of the maxilla (character 40), c) a short coracoid-mesocoracoid articular process (character 41), d) angular anterodorsal margin of the dorsal winglike blade of the anterior ceratohyal (character 31) and e) narrow and acute termination of the posteriorly-directed lateral process of the coracoid.

Two major monophyletic subgroups are present in clade K: the *omphus* species group (clade L) and the *spinosus* species group (clade O). Seven synapomorphies were found for clade L but five of them (characters 46 to 50, incl.) are convergent with other subgroups of *Polyipnus* and/or are reversed within this clade (characters 33 and 50). However the four contained species do share a unique structure of the first dorsal-fin pterygiophore (character 44) and a lack of overlap of the ossified portions of the ectopterygoid and palatine bones (character 45).

Within clade L, *P. omphus* is the sister group of the remaining three miniature (sensu Weitzman and Vari, 1988) species *P. aquavitus, P. unispinus* and *P. danae* (collectively clade M). None of these three species exceeds 40 mm SL (character 58) and, based on the small number of specimens that were examined internally, they all attain sexual maturity by about 25 mm SL. In the context of the cladogram such size reduction as well as body elongation is considered paedomorphic (sensu Fink, 1981, 1982, 1988; Kluge, 1988). Some of the other derived features of these miniature species may also be paedomorphic: the perichondral ossifications of the anal-fin distal radials are reduced in size (character 53) and the radials themselves are spherical.

The *P. spinosus* species group, referred to by Baird (1971), Borodulina (1979) and Harold (1989) as the *spinosus* species complex, is a clade of 14+ Indo-Pacific species. The six species comprising the group were originally united by Baird on the basis of eight characters: a) "greater development of the posttemporal spine complex," which I interpret to mean more than one spine present (character 76), b) otolith structure (attributed by Baird, 1971 to Weitzman, pers. comm.), c) presence of four hypural elements (i.e., hypurals 3 through 6 separate), d) ventral surface of the dentary serrate (character 74), e) "spine-bearing" abdominal keel plates (i.e., PV photophore scales denticulate; character 73), f) second and third preterminal neural spines wedge-shaped, g) "extension of the cleithrum below the pectoral fin relatively more broadened" and h) reduction of the anal-fin pterygiophore hiatus. Of these characters, a, d and e (characters 76, 74 and 73, resp.) appear to be valid synapomorphies of the much larger (14 species) *spinosus* species group recognized here. Characters c, f, g and h exhibit too much variation within and among species to be interpreted at this level. Adequately preserved otoliths were not available for study so appraisal of b above is not possible.

Among new characters found that support monophyly of the *spinosus* species

group are ventral preopercular spine shape (character 72), ventral limb of the posttemporal serrate (character 75), lack of an anterior median lamella on the first proximal radial of the dorsal fin (character 77), elongate and very narrow ectopterygoid (character 13), broadly arced ectopterygoid median ridge (character 79), secondary lateral frontal keel disjunction (character 80), modification of the posterior shelf of the epioccipital into a cuplike fossa (character 81) and presence of numerous minute densely-packed teeth on the ceratobranchial of the fifth branchial arch (character 82).

Baird (1971) suggested that there were two distinct lineages within his *spinosus* complex on the basis of posttemporal morphology and, as key characters, the number of anal (ACB) photophores and the distance between the anal and subcaudal (ACC) photophore clusters. One of these groups, with three posttemporal spines, a high ACB number with a correspondingly small ACB-ACC space was referred to the *spinosus* subgroup by Borodulina (1979). The remaining species, according to Baird characterized by "peculiar reductions" of the posttemporal spines, were subsequently named the *indicus* subgroup (*P. oluolus, P. nuttingi, P. indicus,* and by Baird's criterion, the new species *P. asper*). According to the present analysis, the "*indicus* subgroup" is not monophyletic but the "*spinosus* subgroup" is (Clade S, *P. inermis* to *P. tridentifer*). Members of the "*indicus* subgroup" form successive sister groups to the remaining members of the *spinosus* species group (clade O).

Taxonomic Revision

Polyipnus Günther, 1887

Polyipnus Günther, 1887: 170 (type species *Polyipnus spinosus* Günther, 1887 by monotypy).—Fowler, 1936: 240.—Schultz, 1938: 135; 1961: 620.—Baird, 1971: 79.—Eschmeyer, 1990: 325.
Acanthopolyipnus (subgenus) Fowler, 1934: 257 (type species *Polyipnus fraseri* Fowler, 1934 by monotypy).

Diagnosis.—Synapomorphies: Epioccipital with shelflike posterior process (char. 1); anterior ceratohyal foreshortened and compressed (char. 2); urohyal large and dorsoventrally expanded (char. 3); vertical step between ACB photophores three and four (char. 4); presence of L photophore; modified anterior dorsal-fin pterygiophore, with bispinous process (char. 6). Other characters, in combination: Body deep (42.4–76.7% SL) and compressed. Eyes large (orbit length 11.1–23.0% SL) and laterally positioned. Photophores: PV (10), OVA (2) + 1, OVB 1 + 1 + 1, L 1, AC variable among species, never originating anterior of anal-fin origin; ACA 0, 1 + (2), (3) or 1 + 1 + 1, ACB (4–14), ACC (4). One to three relatively large posttemporal spines present. Frontal bones with one transverse and two longitudinal external keels. Distal radials of dorsal and anal fins mainly cartilaginous but with rounded ossified lateral plates.

Description.—Maximum body size about 100 mm SL. D 10–16. A 11–20. P 11–16. V 6/7. C 8 + 9. GR 3–8 + 7–16 = 11–30. Vertebrae 31–36. (Frequency distributions of meristic characters: dorsal-fin rays, Table 1; anal-fin rays, Table 2; pectoral-fin rays, Table 3; ACB photophores, Table 4; vertebrae, Table 5; gill rakers on first gill arch, Table 6). Body compressed. Anterior body profile broadly elliptical to subrectangular. Flank scales diaphanous, sheetlike, frequently deciduous. Modified scales covering photophores, in many species with denticles laterally and/or ventrally. Frontal with a longitudinal keel usually adjoining and appearing continuous with parietal keel. Additional keels extending anterolaterally from parietal onto frontal, two frontal keels connected by transverse keel. Margins

Table 1. Frequency distribution of number of dorsal fin rays in the species of *Polyipnus*

Species	Number of dorsal fin rays						
	10	11	12	13	14	15	16
kiwiensis			5				
aff. *kiwiensis*		5	2				
matsubarai			7	2			
meteori		4	14				
ovatus			1				
ruggeri			4				
asteroides			1	10	5	2	
bruuni			1				
clarus					3	10	3
laternatus[c]			4	10	11	1	
polli				1	10	1	
triphanos		12	16				
aff. *triphanos*				1			
aquavitus			17	20	2		
danae		1	1	3			
omphus					8	3	
unispinus		3	12	2			
asper			15	14			
elongatus				4	1		
fraseri	2						
indicus			1	10	4		
inermis			6	X[a]			
nuttingi			2	19	4		
oluolus					1		
parini			1	1			
paxtoni		2	6	3			
soelae			11	15			
spinifer			6	19	2		
spinosus			1	1			
spinosus[c]			1	15	4	1	
stereope				6[c]			
tridentifer				9	9		

Literature values from: [a] Borodulina, 1981; [b] Baird, 1971; [c] Schultz, 1961; [d] Borodulina, 1979; [e] Schultz, 1938.

of dentary and premaxilla with two or three rows of minute conical to recurved teeth. Maxillary teeth smaller, much more widely spaced than other jaw teeth. Palatine teeth present or absent. Vomerine dentition various.

Posttemporal limbs elongate and with one to three posteriorly-directed spines at angle. Ventral limb of posttemporal fused with supracleithrum. Cleithrum with fanlike pectoral shield has one to three rows of minute spines evenly distributed along its ventral margin. Cleithrum terminates anteroventrally in bipartite "preabdominal" spine (terminology of Schultz, 1961). Preopercle usually with two spines at angle. Ventral preopercular spine largest and of various shapes and attitudes. Dorsal preopercular spine usually very short and indistinct. A third, posterior, preopercular spine occurs in one species (*P. fraseri* Fowler, 1934). Pelvic skeleton with paired iliac ("postabdominal" of Schultz, 1961) spines. First anal-fin proximal radial with median and expanded lateral lamellae, some species with paired spines originating on the ventral surface of this modified pterygiophore.

Photophores: IP (6). BR (6). ORB 1. OP 1 + 1 + 1. OVA (2) + 1. OVB 1 + 1 + 1. L 1. Following photophore series with (in many species) denticles originating on covering scales: PV (10). VAV (5). ACA 1 + (2), (3), 1 + 1 + 1 or 0, ACB (4–14), ACC (4).

Table 2. Frequency distribution of number of anal fin rays in the species of *Polyipnus*

	Number of anal fin rays									
Species	11	12	13	14	15	16	17	18	19	20
kiwiensis					1	2	2			
aff. *kiwiensis*						1	6			
matsubarai							10			
meteori						8	7			
ovatus								1		
ruggeri							3	1		
asteroides						10	7			
bruuni					1					
clarus						9	8			
laternatus[c]					2	15	9	1		
polli						8	4			
triphanos					1	3	7	4		
aff. *triphanos*								1		
aquavitus				2	19	5				
danae					2	2		1		
omphus						3	5	1		
unispinus			8	7	1					
asper					21	7	1			
elongatus							1	1	2	1
fraseri	1	1								
indicus					8	7				
inermis[a]						5	1			
nuttingi					10	13	2			
oluolus				1						
parini							2			
paxtoni					2	1	6	2		
soelae					12	12	2			
spinifer					6	15	5	2		
spinosus					2					
spinosus[c]				2	11	5	4			
stereope					2	4				
tridentifer[d]						7	15	2		

[a,b,c,d,e] Defined in Table 1.

Dorsal dark pigment saddle present; ventral margin with a descending, ventrally truncate bar and various undulations, frequently diagnostic of species. Melanic pigment also associated with dorsal and lateral surfaces of head, photophore tissues, fin bases and body-trunk myosepta.

Remarks.—Baird (1971: 79), in his diagnosis of the genus, listed four postabdominal spines as characteristic of *Polyipnus*. Whether applying the terminology of Schultz (1961) or Baird (1971) there are only two postabdominal (iliac) spines in all species. This must be an editorial error unless Baird was including as postabdominal the paired "preanal" spines that originate on the first anal-fin pterygiophore in several *Polyipnus* species (e.g., *P. asteroides, P. laternatus*).

Among putative shared derived characters listed by Weitzman (1974) that support monophyly of the three hatchetfish genera, *Polyipnus, Argyropelecus* and *Sternoptyx,* is the lack of an antorbital bone. Most *Polyipnus* species recognized here do have an antorbital although in many cases (esp. *spinosus* species group) it is highly reduced. In his morphological study of *Polyipnus,* Weitzman (1974) examined one of these species (*P. tridentifer* McCulloch, 1914 from the Philippines = *P. spinifer* Borodulina, 1979) and three others in which this bone

Table 3. Frequency distribution of number of pectoral fin rays in the species of *Polyipnus*

Species	Number of pectoral fin rays					
	11	12	13	14	15	16
kiwiensis					3	1
aff. *kiwiensis*			1	4	2	
matsubarai		1	4	4		
meteori				11	3	
ovatus				1		
ruggeri				4		
asteroides				12	3	
bruuni				1		
clarus			2	10	2	
laternatus[c]		1	6	10		
polli			9			
triphanos			6	7		
aff. *triphanos*				1		
aquavitus		17	6	1		
danae	3	2	2			
omphus			2	9		
unispinus		8	6			
asper		15	13			
elongatus		1	4			
fraseri				2		
indicus		2	6	7		
inermis[a]				4	4	
nuttingi		3	9	2		
oluolus			1			
parini				1		1
paxtoni			4	7		
soelae		8	19			
spinifer			19	9		
spinosus			1	1		
spinosus[e]			6	5	1	
stereope[c]			6	16	14	1
tridentifer		4	19	1		

[a,b,c,d,e] Defined in Table 1.

is reduced or likely absent. The significance of finding an antorbital bone in *Polyipnus* is in corroboration of the sister group relationship of *Sternoptyx* and *Argyropelecus* proposed by Weitzman (1974) on the basis of other characters. Loss of the antorbital should now be viewed as derived at that level.

Within the genus there are four major clades, referred to species groups below, in which there is considerable diversification of whole-body form and of specific characters and character complexes. Some of the notable derived features and the species groups in which they appear are: a median row of large fanglike vomerine teeth and extreme undulation of the dorsum pigment margin (*meteori* species group), extreme elevation of ACA photophores and their occurrence in a combined organ (*asteroides* species group), body miniaturization and elongation and posttemporal spine elongation (species *omphus* group), and proliferation of posttemporal spines and denticles associated with any of the ventral photophores posterior to the cleithrum (*spinosus* species group).

Baird (1971) recognized 16 *Polyipnus* species in three species complexes (*P. spinosus, P. asteroides* and *P. laternatus* complexes). Including the contributions of Borodulina (1979, 1981), Harold (1989, 1990a) and Aizawa (1990) there are 30 species recognized here (plus one undescribed, Last and Harold, submitted MS) in four monophyletic species groups. Schultz (1961) used the term "com-

Table 4. Frequency distribution of number of ACB photophores in the species of *Polyipnus* (specimens > 25 mm SL except *bruuni* holotype)

Species	Number of ACB photophores										
	4	5	6	7	8	9	10	11	12	13	14
kiwiensis					1	6	X[b]				
aff. *kiwiensis*						7					
matsubarai					1	9					
meteori				1	5	2					
ovatus						1					
ruggeri					3	1					
asteroides					1	15	1				
bruuni				1							
clarus					2	13	2				
laternatus[c]						1	17	10	3		
polli				10	2						
triphanos				1	3	9	3				
aff. *triphanos*					1						
aquavitus						5	13	1			
danae								3	4		
omphus							3	4	1		
unispinus					4[e]	7	5				
asper					21	8					
elongatus										3	2
fraseri	2										
indicus				1	14	4					
inermis[a]					4	3	1				
nuttingi				1	22	6					
oluolus			1								
parini							1	1			
paxtoni							2	8	1		
soelae								11	12	3	
spinifer								8	13	5	
spinosus							2				
spinosus[c]						3	14	2			
stereope						2	5	1			
tridentifer[d]							1	12	24	23	3

[a,b,c,d,e] Defined in Table 1.

plex'' with reference to *Polyipnus* originally only to indicate uncertainty about delimitation of species (especially *P. spinosus* and *P. stereope*).

Key to the Species of Polyipnus

1A. L and third OVA photophores both displaced dorsally, and isolated, level with or dorsal to ACA; lateral pigment bar present, varying from a slight undulation of the dorsum pigment margin to a long, tapered bar extending ventrally to the lateral midline (Figs. 1, 2) (virtually absent in *P. unispinus*) 2

1B. L and third OVA photophores not displaced dorsally: L adjacent to anterior VAV; third OVA photophore at about level of second; lateral pigment bar absent .... *Polyipnus* sp. B (Last and Harold, MS) (western Coral Sea, off Queensland)

2A. Posttemporal bone with coarsely serrate external keels and two or three posteriorly-directed spines; ventral margins of PV photophore scales (abdominal keel) with numerous denticles 3

2B. Posttemporal bone with smooth or finely serrate external keels and a single posteriorly-directed spine; ventral margins of PV scales smooth (except *P. unispinus* which has minute denticles) 16

3A. Ventral margin of PV photophore scales rectangular and finely denticulate 4

Table 5. Frequency distribution of number of vertebrae in the species of *Polyipnus*

Species	Number of vertebrae 30	31	32	33	34	35	36
kiwiensis			X[b]	2	X[b]		
matsubarai				5			
meteori				5			
ovatus				1			
ruggeri				1			
asteroides		2					
bruuni				1			
clarus		2	2	2			
laternatus[c]			3	1			
polli		1	1				
triphanos		1		6			
aff. *triphanos*				1			
aquavitus		1		1	3	1	
danae							2
omphus				2	2		
unispinus[c]						1	9
asper				2			
elongatus						2	
fraseri		1	1				
indicus			3	1			
inermis					1		
nuttingi[c]				24	3		
oluolus				1			
parini						2	
paxtoni				1	2	1	
soelae				2	2		
spinifer					2	3	
spinosus			1	1			
spinosus[c]				8	1		
stereope[c]				3			
tridentifer[d]					4	1	

[b,c,d] Defined in Table 1.

3B. Ventral margin of PV photophore scales with triangular extensions, each with one or two denticles at apex .... *P. oluolus* Baird, 1971 (Marshall Islands)

4A. ACB photophores 7–13 (specimens >20 mm SL); one lateral dark pigment bar 5

4B. ACB photophores 4 (specimens >20 mm SL); two lateral dark pigment bars .... *P. fraseri* Fowler, 1934 (Philippine Sea)

5A. Ventral posttemporal spine relatively large, its length greater than or equal to half of the length of dorsal spine (Fig. 5A); posttemporal spines 3 6

5B. Ventral or basal posttemporal spine short, length less than half of the length of dorsal spine (Fig. 5B); posttemporal spines 2 or 3 12

6A. Posttemporal spines subequal, tridentlike 7

6B. Posttemporal spines of various lengths, dorsal and ventral spines longest, median much shorter than ventral spine 9

7A. Gap separating ACB and ACC photophore clusters about equal to length of ACC cluster; lateral dark pigment bar long, reaching lateral midline; ventral surface of ACC photophore scales smooth, without denticles 8

7B. Gap separating ACB and ACC photophore clusters about equal to width of one ACC photophore; lateral dark pigment bar short, not reaching midline; ventral surface of ACC photophore scales denticulate .... *P. tridentifer* McCulloch, 1914 (Great Australian Bight)

8A. VAV and ACB photophore scales smooth, without denticles; ACB photophores 8 or 9; gill rakers 23–26 .... *P. inermis* Borodulina, 1981 (Sala-y-Gomez Ridge, eastern South Pacific)

Table 6. Frequency distribution of the number of gill rakers on the first branchial arch for *Polyipnus* species

Species	Number of gill rakers																			
	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
kiwiensis						1	3	1												
aff. *kiwiensis*						5	2													
matsubarai												6	1	2						
meteori			1	2	1	1	7	1												
ovatus								1												
ruggeri							2	2												
asteroides										1	2	1	7	4						
bruuni									1											
clarus									6	6	8									
laternatus						1	5	4	8	1[c]	2[c]	1[c]								
polli										6	4	2								
triphanos				1	4	12	6	1	4											
aff. *triphanos*										1										
aquavitus			5	28	2															
danae	3	4																		
omphus							1	3	4	2	1									
unispinus	15	2																		
asper							6	11	9	2										
elongatus												1	2	1						
fraseri									1	1										
indicus									2	7	1									
inermis												4	2	X[a]	X[a]					
nuttingi											1	3	9	11	3					
oluolus									1											
parini																		1		1
paxtoni													4	2						
soelae										10	7	7	2							
spinifer										1	2	3	5	13	2					
spinosus									1	1										
spinosus[c]							4	8	3											
stereope													1	1						
stereope[c]													1	6	8	11	5	6	3	
tridentifer[d]										1	4	14	13	1						

[a,c,d] Defined in Table 1.

8B. VAV and anterior ACB photophore scales denticulate; ACB photophores 10; gill rakers 28 (holotype) or 30 .... *P. parini* Borodulina, 1979 (western Pacific)

9A. ACC photophore reflectors separated by distinct gaps; ACB photophores 11–14; lateral pigment bar short and triangular; caudal peduncle elongate, longer than deep 10

9B. ACC photophore compact, reflectors not separated by distinct gaps; ACB photophores 9–11; lateral pigment bar tapered ventrally, approaching but not reaching lateral midline; caudal peduncle deep, about as deep as long 11

10A. Anterior ACB photophore scales each with 3–6 denticles; ventral and ventrolateral keels of dentary serrate .... *P. spinifer* Borodulina, 1979 (South China Sea to Japanese Archipelago)

10B. Anterior ACB photophore scales smooth or with at most a single denticle; ventrolateral keel of dentary smooth, nonserrate .... *P. soelae* new species (eastern Indian Ocean and Indonesia)

11A. Gill rakers 24–28; ACB photophores 9–11 .... *P. stereope* Jordan and Starks, 1904 (Japanese Archipelago)

11B. Gill rakers 19–23; ACB photophores 10–12 .... *P. spinosus* Günther, 1887 (eastern Indonesia)

12A. Long, broad lateral dark pigment bar extending ventrally at least to lateral midline; anal rays 15–18; ACB photophores 7–12 13

12B. Lateral dark pigment bar approaches but does not reach lateral midline; anal-fin rays 18 or 19; ACB photophores 13 or 14 .... *P. elongatus* Borodulina, 1979 (western Coral Sea)

13A. ACB photophores 7–10; posttemporal usually with 2 spines, 1 long dorsal and 1 much shorter basal spine; ACB photophore scales smooth or with 1–3 denticles per scale 14

13B. ACB photophores 11–12, occasionally 10; posttemporal with 3 spines, 1 long dorsal with subequal median and ventral spines; ACB photophore scales each with more than 3 long denticles originating on lateral scale flanges .... *P. paxtoni* Harold, 1989 (western Coral Sea)

14A. ACC photophore scales denticulate; dorsal posttemporal spine long, length at least twice dorsal spinous process height; lateral dark pigment bar extending ventrally no further than level of center of orbit 15

14B. ACC photophore scales smooth, without denticles; dorsal posttemporal spine short, length about equal to dorsal spinous process height; lateral dark pigment bar extending ventrally beyond level of center of orbit .... *P. nuttingi* Gilbert, 1904 (Hawaiian Islands)

15A. Longitudinal parietal keel evenly serrate and continuous with frontal keel (see Fig. 6C); ACB photophore scales smooth, without denticles; palatine teeth present .... *P. indicus* Schultz, 1961 (western Indian Ocean)

15B. Longitudinal parietal keel discontinuous, posterior region forming 2 minute conical spines directed towards anterior and posterior; ACB photophore scales each with 1 to 3 denticles (specimens over 40 mm SL); palatine teeth absent .... *P. asper* new species (Andaman Sea, eastern Indian Ocean)

16A. Ventral preopercular spine prominent, tapered; ACB photophores 9–13 (specimens over 25 mm SL) and without a conspicuous step between photophores #3 and #4; posttemporal spine long and needlelike 17

16B. Ventral preopercular spine reduced and imbedded within ventral lamella of preopercle (*P. surugaensis* not examined); ACB photophores 7–10 and with a conspicuous step between #3 and #4; posttemporal spine short and stout, expanded basally 21

17A. Gill rakers 16–21; posttemporal spine of moderate length (5.7–10.7% SL); ACC photophore reflectors in contact or separated by gaps less than the width of one photophore; body size moderate, reaching at least 45 mm SL 18

17B. Gill rakers 11–15; posttemporal spine highly elongate (10.0–16.1% SL); ACC photophore reflectors separated by gaps greater than width of one photophore; miniature species, not known to exceed 35 mm SL 19

18A. ACA photophores elevated relative to ACB #1 by a distance greater than twice the horizontal width of one photophore; ACA #1 located ventrally to #2; caudal peduncle profile rectangular, slightly expanded posteriorly; lateral dark pigment bar short, tapered and not bordered posteriorly by an elongate predorsal notch .... *P. laternatus* Garman, 1899 (western Atlantic)

18B. ACA photophores elevated relative to ACB #1 by a distance less than the horizontal width of one photophore; ACA #1 at about same elevation as or dorsally of ACA #2; caudal peduncle profile tapered posteriorly; lateral pigment bar short but ventral termination blunt,

and bordered posteriorly by an elongate, anterodorsally-arced predorsal notch .... *P. omphus* Baird, 1971 (equatorial Indo-Pacific)

19A. Gill rakers 13–15; lateral pigment bar short, hemispherical; caudal peduncle rectangular, compressed .... *P. aquavitus* Baird, 1971 (eastern Indonesia, Coral and Tasman Seas)

19B. Gill rakers 11 or 12; lateral pigment bar short and triangular or absent; caudal peduncle highly elongate, rodlike 20

20A. Ventral margins of PV photophore scales with minute denticles; ACB photophores 9–10, posterior 4–6 not visibly interconnected; ventral margin of pigment saddle parallel to dorsal surface of body, without lateral bar or undulations .... *P. unispinus* Schultz, 1938 (Indonesia, Coral and Tasman Seas)

20B. Ventral margins of PV photophore scales smooth, without denticles; ACB photophores 11 or 12, only posterior 1 or 2 photophores at most not visibly interconnected; ventral margin of dorsum pigment with a minute broad triangular lateral pigment bar ventral to dorsal fin origin .... *P. danae* Harold, 1990 (South China Sea)

21A. ACA photophore #2 slightly ventral to and not connected to #3; 1 or 2 rows of large, recurved teeth present on posteromedian shaft of vomer 27

21B. ACA photophore #2 similarly elevated and connected to #3 in a common organ; no teeth present on posteromedian shaft of vomer 22

22A. Anal-fin pterygiophore spines present; gill rakers 19–24 23

22B. Anal-fin pterygiophore spines absent; gill rakers 14–20 25

23A. OVB photophores in a "V" configuration; anal-fin base highly convex, with pterygiophores extending noticeably beyond ventral margins of ACB photophores; ACB 7/8 .... *P. polli* Schultz, 1961 (eastern Atlantic)

23B. OVB photophores in an anteriorly-inclined straight line or #2 and #3 at same elevation with #1 located dorsally; anal-fin base nearly straight, pterygiophores not extending noticeably beyond ventral margins of ACB photophores; ACB 8–10 24

24A. Lateral pigment bar long and tapered, extending ventrally to lateral midline; overall pigmentation in preservative very dark, body-trunk myosepta with heavy concentrations of dark pigment; anal-fin pterygiophore spines short and basally expanded; ACA #3 elevation (relative to ACB #1) 6.9–7.9% SL; gill rakers 20–24 .... *P. asteroides* Schultz, 1938 (Caribbean Sea and off Greater Antilles)

24B. Lateral pigment bar short and triangular, extending ventrally less than half way to lateral midline; overall pigmentation in preservative pale, body-trunk myosepta diffusely delineated with dark pigment; anal-fin pterygiophore spines long and needlelike; ACA #3 elevation (relative to ACB #1) 4.9–6.6% SL; gill rakers 19–21 .... *P. clarus* new species (western Atlantic, Caribbean Sea to Scotian Shelf)

25A. Ventral margin of dark dorsomedian pigment from caudal peduncle to dorsal-fin origin parallel to dorsal surface of body (postdorsal notch absent); ACA photophores in a horizontal straight line and united in a common organ .... *P. bruuni* new species (western Indian Ocean, off Kenya)

25B. Ventral margin of dark dorsomedian pigment arched dorsally ventral to dorsal-fin insertion (a broad postdorsal notch present); ACA photophore #1 ventrally displaced relative to #2 by a distance greater than the diameter of one ACA photophore 26

26A. OVB photophores roughly in a "V" configuration, and the first slightly elevated relative to the third; predorsal pigment notch a shallow arc, not reaching dorsal midline .... *P. triphanos* Schultz, 1938 (South China Sea, Indonesia and Coral Sea)

26B. First and second OVB photophores at about the same level, the third elevated, at about level of anterior VAV; predorsal pigment notch elongate, reaching dorsal midline anterior to dorsal fin origin .... *P. surugaensis* Aizawa, 1990 (Suruga Bay, Japan)

27A. Gill rakers 22–24; lateral pigment bar very narrow, its width ventrally less than the width of L photophore .... *P. matsubarai* Schultz, 1961 (northwest Pacific, off Japan, Philippine Sea)

27B. Gill rakers 13–18; lateral pigment bar broad, its width ventrally greater than the width of L photophore 28

28A. Lateral pigment bar reduced or absent; OVB photophores arranged in a horizontal line .... *P. ruggeri* Baird, 1971 (Tasman Sea)

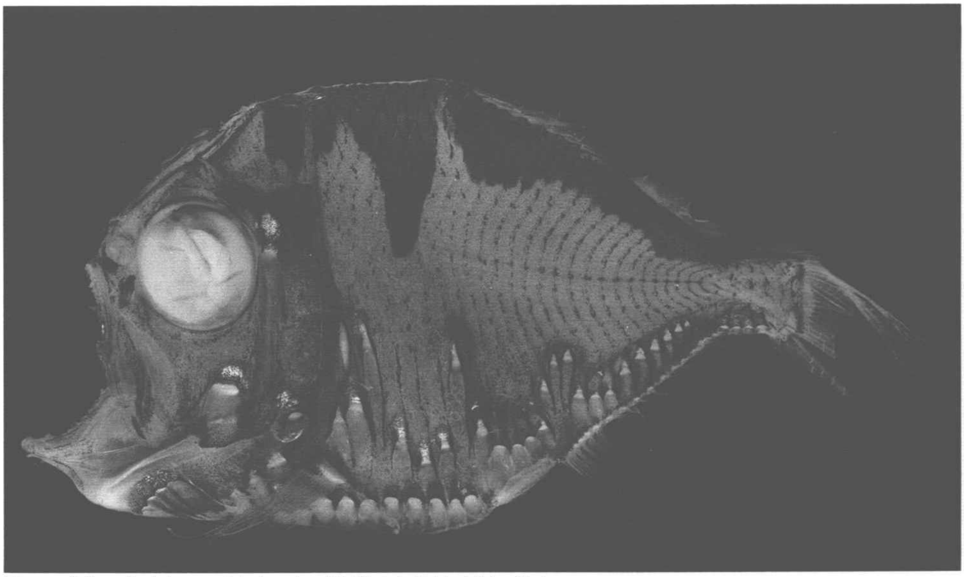

Figure 20. *Polyipnus kiwiensis*, AMS I.24501-004, 60.3 mm.

28B. Lateral pigment bar well-developed and extending ventrally at least to lateral midline; OVB photophores variously arranged but never in a horizontal line 29

29A. Posttemporal spine with a pronounced anterodorsal barb (see Fig. 5C); ventral margin of pigment saddle with an abrupt postdorsal notch; lateral pigment bar ventrally tapered; indistinct dorsal step between photophores ACB #3 and #4 .... *P. meteori* Kotthaus, 1967 (equatorial and tropical Indo-Pacific)

29B. Posttemporal spine anterodorsal surface without a barb; ventral margin of pigment saddle with broad postdorsal notch; lateral pigment bar terminating bluntly near lateral midline; pronounced dorsal step between photophores ACB #3 and #4 30

30A. Anal-fin rays 15–17; pectoral-fin rays 15–16; lateral ridges of preopercle smooth, nonserrate .... *P. kiwiensis* Baird, 1971 (Tasman Sea and off New Zealand)

30B. Anal-fin rays 18; pectoral-fin rays 14; lateral keels of preopercle with shallow serrations around angle .... *P. ovatus* new species (South China Sea, off northern Philippines)

Polyipnus meteori species group

Five species of the Indo-Pacific region: *P. kiwiensis, P. matsubarai, P. meteori, P. ovatus* and *P. ruggeri.*

Polyipnus kiwiensis Baird, 1971
Figure 20

Polyipnus kiwiensis Baird, 1971: 103–104 (holotype fig. 79).—Paxton et al., 1989: 192 (part, specimens from northwest Australian shelf questionably identified as *P. kiwiensis*).—Harold, 1990b: 515.—Aizawa, 1990: 97.

Type Material.—Holotype: NMNZ 4802 (1, 59.5 mm).

Other Material.—AMS I.15984-002 (1, 48.6 mm). AMS I.24496 (1, 73.6 mm). AMS I.17863 (1, 82.0 mm). AMS I.19855 (1, 79.4 mm). AMS I.17861-001 (1, 73.8 mm). AMS I.17864-003 (1, 77.3 mm). AMS I.24501-004 (1, 60.3 mm). WAM P28071-001 (7, 54.0–72.0 mm).

Diagnosis.—Autapomorphies: dorsal spinous process with paired lateral ridges. Maxillary postpalatinad facet (Stiassny, 1986) reduced, inconspicuous. Dorsal

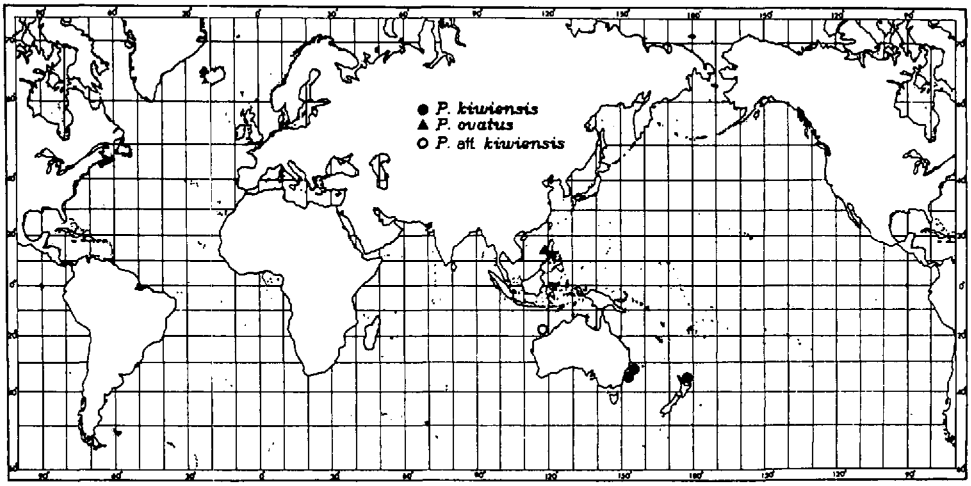

Figure 21. Collection station localities for *P. kiwiensis*, *P. ovatus*, and *P.* aff. *kiwiensis*, *P. meteori* species group.

preopercular spine and serration of proximal lamellar ridge of preopercle absent. Other characters, in combination: Gill rakers 16–18. Anal-fin rays 15–17. Pectoral-fin rays 15/16. Lateral pigment bar long and broad, usually reaching lateral midline. One short posttemporal spine. Anal-fin pterygiophore spines and photophore scale denticles absent. ACA photophores separate, #2 and #3 conspicuously elevated relative to first ACB. ACB 8–10. Teeth present on posteromedian vomerine process.

Description.—Maximum adult body size 82.0 mm SL. D (12) 11–12. A (17) 15–17. P 15–16. V 7. GR 5/6 + 11/12 = (17) 16–18. Vertebrae (34) 33.

Ventral margins of all photophore scales smooth, without denticles. OVB 1 + 1 + 1, in a "V" configuration but with #1 elevated, less than the diameter of one photophore, relative to #3. ACA 1 + 1 + 1, not united in a common organ, increasing in elevation from anterior to posterior and #2 and #3 usually proximal to one another. ACB (10, according to illustration of holotype in Baird, 1971: fig. 79; 8–9), with a dorsal step between #3 and #4. ACC (4), compact.

Similar Species.—Polyipnus kiwiensis most closely resembles *P. ovatus,* both of which have a long lateral pigment bar with a rounded terminus and a very broad postdorsal pigment notch. Characters distinguishing *P. kiwiensis* from *P. ovatus* are its nonserrate preopercular ridges, low numbers of gill rakers (15–17 as compared with 18) and anal-fin rays (15–17 as compared with 18), and higher pectoral-fin ray counts (15/16 as compared with 14). The pattern of pigmentation is also similar to *P. triphanos, P.* aff. *triphanos* and *P. surugaensis; P. kiwiensis* is distinguished by the 1 + 1 + 1 ACA photophore configuration [as compared with 1 + (2)] and presence of posteromedian vomerine teeth.

Distribution.—Polyipnus kiwiensis is restricted to the Tasman Sea off the southeast coast of Australia and continental slope areas of New Zealand (Fig. 21). A disjunct population of this species has been reported off the northwest coast of Australia (Paxton et al., 1989). Specimens from that area are referred to *P.* aff. *kiwiensis.*

Remarks.—This species was originally thought by Baird (1971) to be endemic to

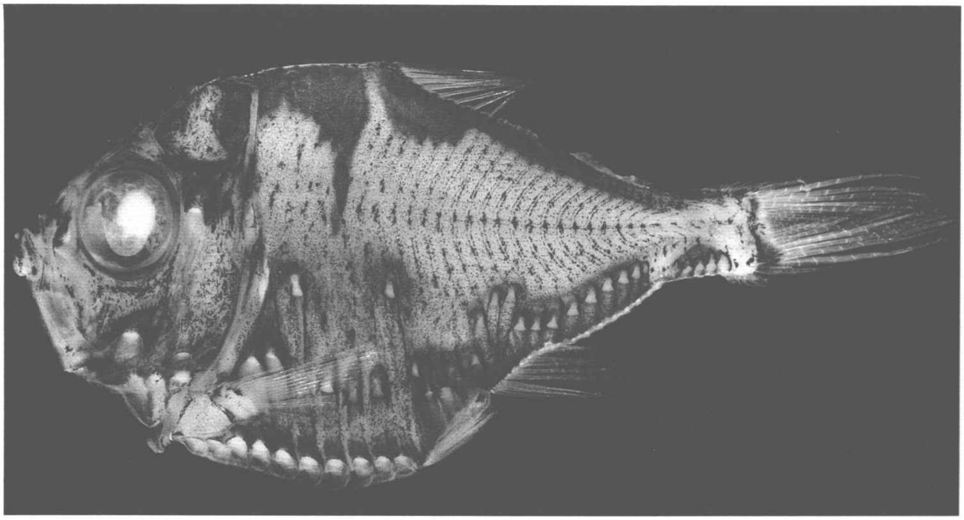

Figure 22. *Polyipnus matsubarai*, ROM uncat., 42.6 mm.

the New Zealand slope. The range is here expanded to encompass both east and west sides of the Tasman Sea. Seven specimens from the northwest Australian shelf (*P.* aff. *kiwiensis;* WAM P28071-001) differ in some meristic character values from the Tasman Sea population. Further study may reveal there to be an undescribed species here but this apparent differentiation is, for the present, best regarded as geographic variation.

Polyipnus matsubarai Schultz, 1961
Figure 22

(non) *Polyipnus asteroides*: Matsubara, 1941: 2; 1950: 192.
Polyipnus matsubarai Schultz, 1961: 641–642 (holotype fig. 17); 1964: 267.—Baird, 1971: 101–102 (fig. 77).—Kubota et al. 1984: 43–50 (fig. 1).—Fujii, 1984: 47 (pl. 49N).—Harold 1990a: 1114; 1990b: 515.—Aizawa, 1990: 97.
Polyipnus japonicus Schultz, 1961: 643 (holotype fig. 19); 1964: 268.

Type Material.—Holotype: USNM 179793 (1, 64.0 mm). Paratypes: USNM 179794 (1, 51.5 mm) and FAKU cat. no. unknown (3, 45.0–59.0 mm), collected with holotype (FAKU specimens not seen).

Other Material.—IOAN uncat. (6, 52.3–66.5 mm), 37°27′N 160°00′E, 260-0 m, MVS TIKHIY Sta. 41, 21 May 1979. NMC 79-0009 (1, 96.7 mm). NMC 79-0006 (1, 84.1 mm). NMFSH P-1002 (1, 67.7 mm). NSMT P12415 (1, 25.2 mm). ORIT 2581 (1, 41.4 mm). ORIT 2582 (1, 39.5 mm). ROM uncat. (2, 39.0–42.6 mm), Suruga Bay, Japan, no exact data. SIO H53-367-10A (1, 12.3 mm) (*P. japonicus* Schultz, 1961, holotype). ZMUC P206927) (1, 19.0 mm). ZMUC P206926 (1, 33.0 mm).

Diagnosis.—Autapomorphies: dentigerous UP3 extending onto anterior shaft of third infrapharyngobranchial (PB 3). Transverse and secondary longitudinal frontal keels finely serrate. Lateral pigment bar long and very narrow, extending ventrally of lateral midline. Other characters, in combination: Gill rakers 22–24. One short posttemporal spine. Anal-fin pterygiophore spines and photophore scale denticles absent. ACA photophores separate, #2 and #3 conspicuously elevated relative to first ACB. ACB 8–9. Teeth present on posteromedian vomerine process.

Description.—Maximum adult body size 96.7 mm SL. D (13) 12–13. A (17) 16–17. P (12/13) 12–14. V 7. GR 6/7 + 15/16 = 22–24. Vertebrae (33) 33.

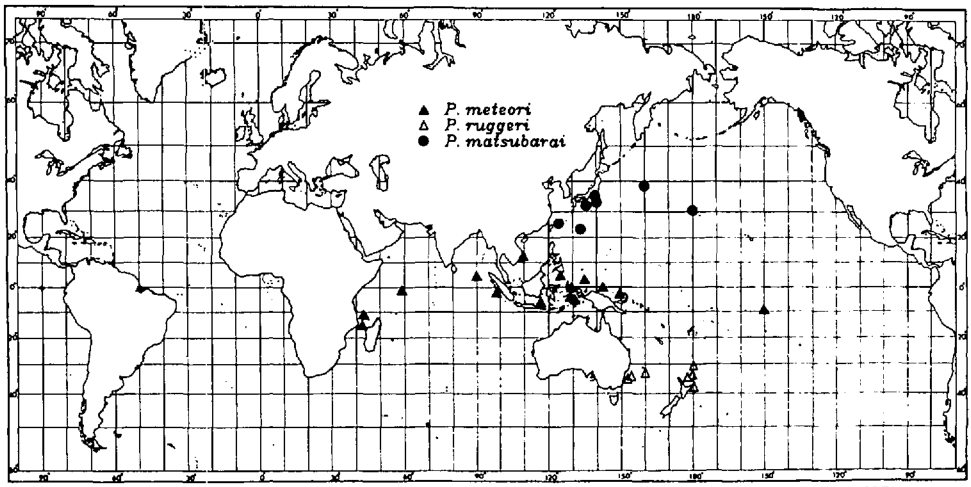

Figure 23. Collection station localities for *P. meteori, P. ruggeri* and *P. matsubarai, P. meteori* species group.

Ventral margins of photophore scales smooth, without denticles. OVB 1 + 1 + 1, arrangement variable but #1 always elevated relative to #2 and #3. ACA 1 + 1 + 1, each isolated, not united in common organ, increasing in elevation incrementally from anterior to posterior. ACB (9, 8–9), with dorsal step between #3 and #4. ACC (4), compact.

Similar Species.—Of the members of the *meteori* species group *P. matsubarai* most closely resembles *P. meteori* in pigmentation, both having a very long narrow lateral band of dark pigment. The postdorsal pigment notch is broad in *P. matsubarai,* however, and not abrupt. *Polyipnus matsubarai* is distinguished from all other members of the species group by its high gill raker counts (22–24 as compared with 13–18, total range).

Distribution.—*Polyipnus matsubarai* is known mainly from the Japanese Archipelago, especially the Suruga Bay area where it is often caught by commercial shrimp trawls (Kubota et al., 1984). Captures have also been made in the Philippine Sea and eastward in the Northwest Pacific Basin near the Hawaiian-Emperor Seamounts (Fig. 23). Bathymetric range is generally shallow; about 80 to 130 m, according to Kubota et al. (1984).

Other *Polyipnus* species occurring in the area are *P. spinifer* and *P. stereope* (both *P. spinosus* species group) and *P. surugaensis.*

Remarks.—The holotype of *P. japonicus* Schultz, 1961 was re-examined during the present study and it appears to be a juvenile or subadult of *P. matsubarai.* The very low number of ACB photophores (4) which Schultz believed was an indication of close relationship with *P. fraseri* is expected in small *Polyipnus* (Harold, 1990b). Baird (1971: 101) listed *P. japonicus* as a junior synonym of *P. matsubarai* but did not comment.

Schultz (1961: 641), who described *P. matsubarai,* discussed the species in terms of differences from *P. asteroides* (Atlantic Ocean), which at the time appeared to be the most similar of the nominal species. It is now recognized that *P. matsubarai* is a northerly representative of the Indo-Pacific *P. meteori* species group.

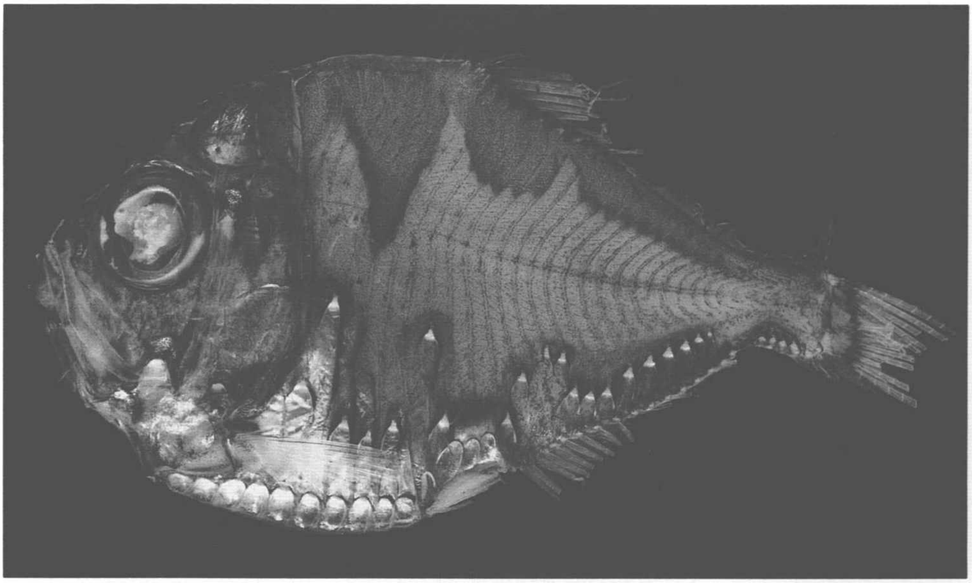

Figure 24. *Polyipnus meteori,* LACM uncat., ALPHA HELIX Sta. 108, 52.0 mm.

Polyipnus meteori Kotthaus, 1967
Figure 24

Polyipnus meteori Kotthaus, 1967: 26–27 (holotype fig. 44; holotype x-radiograph fig. 45; otoliths fig. 46).—Baird, 1971: 104; 1986: 257.—Harold 1990a: 1114; 1990b: 515.—Aizawa, 1990: 97.—Harold, 1993: 125 (infrapharyngobranchials).

Type Material.—Holotype: ZMH 4887 (1, 37.0 mm).

Other Material.—IOAN uncat. (1, 44.1 mm), 05°18'N 125°50'E, 200–0 m, VITYAZ Cr. 57, Sta. 7227, 0212–0312 h, 24 Feb 1975. IOAN uncat. (1, 66.0 mm), 01°43'S, 143°04'E, 0–500 m, VITYAZ Cr. 50, Sta. 7321, 6 Apr 1975. IOAN uncat. (1, 60.5 mm), 05°15'N 124°05'E to 05°20'N 124°02'E, 0–500 m, VITYAZ Cr. 57, Sta. 7231, 2320–0020 h, 25–26 Feb 1975. IOS uncat. (2, 15.7–29.6 mm), 00°03'N 58°03.3'E to 00°32.1'N 58°04'E, 1,200 mwo, R.R.S. DISCOVERY Sta. 5415, 2030–0242 h, 1965. LACM 36143- uncat. (1, 50.8 mm), 04°43'S 129°36'E, 0–1,000 m, ALPHA-HELIX Sta. 108, 0020–0445 h, 8 May 1975. LACM 36063- uncat. (1, 24.8 mm), 00°0.6'S 128°46.3'E, 250–320 m, ALPHA-HELIX Sta. 140, 0203–0310 h, 20 May 1975. LACM 36054- uncat. (2, 21.1–22.6 mm), 04°49.5'S 129°55'E, 0–650 m, ALPHA-HELIX Sta. 76, 0955–1247 h, 27 Apr 1975. MCZ 64694 (1, 18.6 mm). SIO 61-541-10 (1, 29.0 mm). USNM 256965 (1, 21.3 mm). ZMUC P206928 (1, 54.6 mm). ZMUC P206929 (2, 12.8–22.6 mm). ZMUC P206930 (1, 64.1 mm). ZMUC P206931 (1, 37.6 mm). ZMUC uncat. (1, 20.4 mm), 14°16'S 41°48'E, 600 mwo, DANA Sta. 3951 II, 1900–2030 h, 7 Jan 1930. ZMUC uncat. (2, 17.7–21.1 mm), 07°53'S 116°18'E, 600 mwo, DANA Sta. 3800 I, 1925–2125 h, 13 Aug 1929. ZMUC uncat. (1, 15.7 mm), 05°18'N 90°55'E, 2,500 mwo, DANA Sta. 3904 III, 1745–1945 h, 18 Nov 1929.

Diagnosis.—Autapomorphy: Modified first dorsal-fin pterygiophore with two posterior condyles articulating with second pterygiophore. Other characters, in combination: Gill rakers 13–18. Lateral pigment bar long and very narrow, extending ventrally of lateral midline. Abrupt archlike deflection of dorsum pigment ventral margin dorsal to ACA photophores. One short posttemporal spine. Anal-fin pterygiophore spines and photophore scale denticles absent. ACA photophores separate, #2 and #3 conspicuously elevated relative to first ACB. ACB 7–9. Teeth present on posteromedian vomerine process.

Description.—Maximum adult body size 54.6 mm SL. D (12) 11–12. A (16) 16–17. P (15) 13–15. V (6) 6–7. GR 4/5 + 9–13 = (15/13) 14–18. Vertebrae (33) 33.

Ventral margins of photophore scales smooth, without denticles. OVB 1 + 1 + 1, arrangement variable but #1 always dorsally elevated relative to #2 and #3, commonly in a "V" arrangement. ACA 1 + 1 + 1, each isolated, not united in common organ, increasing in elevation incrementally from anterior to posterior. ACB (9; 7–9), with dorsal step #3 and #4. ACC (4), compact.

Similar Species.—Of the members of the *meteori* species group *P. meteori* most closely resembles *P. matsubarai* with regard to body shape and extent of lateral pigmentation but is distinguished by lower gill raker counts (13–18 compared with 22–24) and the presence of an abrupt postdorsal pigment notch. Such a pigmentation pattern is also present in *P. ruggeri* but this species has a highly reduced lateral pigment bar, an unusual convex abdominal profile, and the first and their OVB photophores ventrally, nearly at the level of the second.

Distribution.—*Polyipnus meteori* is more widely distributed longitudinally than any other species in the genus. It was originally known from a single station in the western Indian Ocean off Madagascar but is reported here from the Indo-Malayan Archipelago and as far east as the Line Islands (central Pacific) thus spanning more than 170 degrees of longitutude (Fig. 23). *P. meteori* appears to be restricted to the equatorial region (no captures at latitude greater than 15°). This species has been collected by discrete-depth sampling gear (i.e., RMT-8 net) in Indonesia and the results show that it occurs between 250 and 320 m and between 100 and 290 m at night. The only capture known with certainty to have been made during daylight hours was an open tow to 650 m.

The distribution of *P. meteori* as presently understood is disjunctive. The more likely cause is insufficient collecting effort in the gap areas. Numerous collections in the Indonesian Archipelago show overlap between the range of this wide-ranging species and *P. ovatus, P. triphanos, P. omphus, P. danae, P. aquavitus, P. unispinus, P. danae, P. soelae, P. spinifer* and *P. spinosus.*

Remarks.—One specimen is here tentatively referred to *P.* aff. *meteori* (ZMUC P206930, Java Trench off Sumatra) because of atypical morphometric values and photophore arrangements. Although this specimen possibly represents an undescribed species it is not treated formally here, expecting that material in better condition will eventually be collected (ZMUC P206930 is decalcified and has been badly damaged by fungal infestation).

Polyipnus ovatus new species
Figure 25

Type Material.—Holotype: CAS 33347 (1, 47.0 mm), Pagapas Bay, Philippine Islands (about 13°N 121°E), 194–209 m, 0355–0435 h, 21 Jul 1966.

Diagnosis.—Autapomorphy: Proximal lamellar ridge of ventral and dorsal rami of preopercle serrate. Other characters, in combination: Gill rakers 18. Anal-fin rays 18, Pectoral-fin rays 14. Lateral pigment bar long and broad, usually reaching lateral midline. One short posttemporal spine present. Anal-fin pterygiophore spines and photophore scale denticles absent. ACA photophores separate, #2 and #3 conspicuously elevated relative to first ACB. ACB (9). Teeth present on posteromedian vomerine process.

Description of Holotype.—Maximum adult body size: 47.0 mm SL. D (12). A (18). P (14). V (6). GR (5 + 13) = (18). Vertebrae (33). Body profile anterior of dorsal fin and pelvic fin ovate, acutely tapered posteriorly as far as ACC photophore cluster. Profile of caudal peduncle rectangular, short. Margins of den-

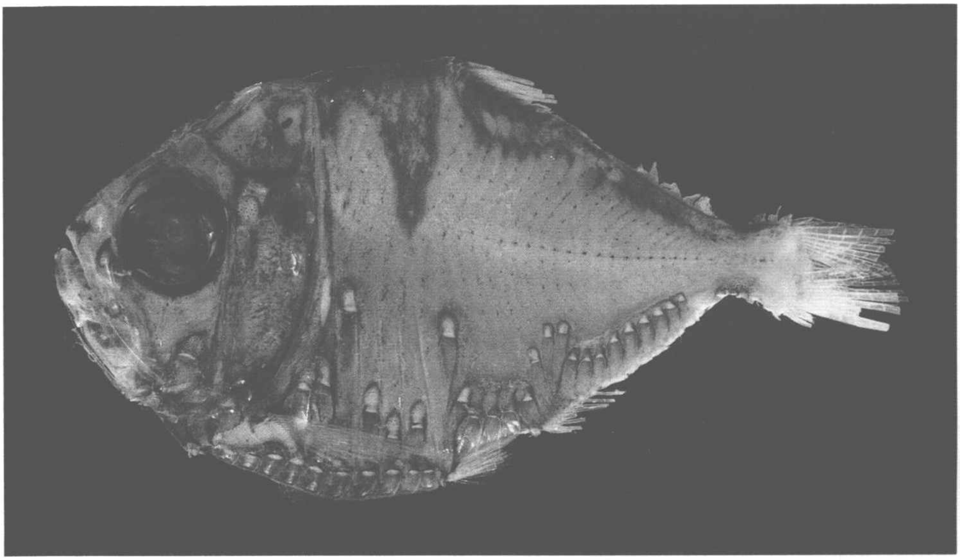

Figure 25. *Polyipnus ovatus*, holotype, CAS 33347, 47.0 mm.

tary and premaxilla with long recurved teeth. Maxilla with shorter conical teeth. Three conical palatine teeth in a median row. Anterolateral processes of vomer each with a patch of two or three recurved teeth. Five recurved fanglike teeth on posteromedian process of vomer in two longitudinal rows. Frontal and parietal keels serrate. Parietal keel terminating anteriorly and posteriorly in spines, anterior spine more than twice the length of posterior spine. Dorsal and ventral limbs of posttemporal nonserrate, supporting short (4.4% SL) dorsally-concave spine. Ventral margin of pectoral shield with 12 or 13 minute triangular spines. Preopercle with two spines: ventral spine straight and short (2.4% SL), ventrally directed, embedded entirely within ventral lamella except conical terminus; dorsal spine short (slightly longer than preopercular serration), triangular, bladelike. Dorsal spinous process smooth and obtusely convex anterodorsally, apically depressed and with two rounded triangular spines, one per side, directed posterodorsally. Anal-fin pterygiophore spines absent.

Morphometric characters (% SL): Head length 35.1, orbit length 14.6, body depth 60.0, caudal-peduncle depth 10.0, caudal-peduncle length 14.1, dorsal-fin length 20.4, anal-fin length 27.2, preanal length 70.2, predorsal length 58.5, preventral length 63.0, postdorsal length 53.2, postanal length 41.7, ACC length 6.1, ACB-C length 3.8.

Ventral margins of photophore scales smooth, without denticles. OVB 1 + 1 + 1, in a "V" configuration but with #1 elevated a distance greater than diameter of one photophore, relative to #3. ACA 1 + 1 + 1, separate, not united in a common organ, increasing in elevation from anterior to posterior and #2 and #3 proximal to one another. ACB (9), with dorsal step between #3 and #4. ACC (4), compact.

Dark pigment saddle with abrupt predorsal and broad postdorsal notches. Long, broad, tapered lateral projection of dark pigment present that terminates ventrally of lateral midline dorsal to OVB photophores.

Similar Species.—Polyipnus ovatus and *P. kiwiensis* are most similar with regard

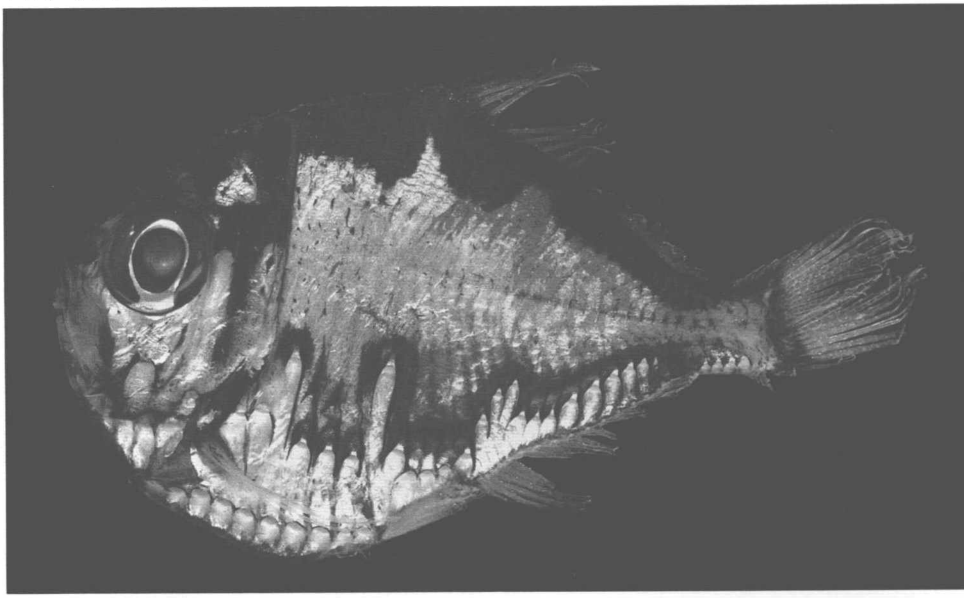

Figure 26. *Polyipnus ruggeri,* AMS I.20066-014, 49.1 mm.

to body shape and pigmentation pattern but clearly distinguished by fin-ray counts; *P. ovatus*: A 18, P 14, V 6 compared with *P. kiwiensis*: A 15–17, P. 15/16, V 7. The pattern of pigmentation is also similar to *P. triphanos* and *P. surugaensis,* species which differ from *P. ovatus* in vomerine dentition and ACA photophore arrangement.

Distribution.—The holotype was collected in Pagapas Bay, west coast of the Philippine Islands (Fig. 21). The depth of capture (194–209 m) is relatively shallow for the genus but since this was a night sample it may result from vertical migration.

Polyipnus ovatus is one of several species now known from the South China Sea (also *P. spinifer, P. danae, P. meteori* and *P. triphanos*). *Polyipnus kiwiensis,* the most closely related species to *P. ovatus,* occurs in the Tasman Sea with a geographic variant off northwestern Australia.

Remarks.—The holotype is remarkably similar in body shape to material here ascribed to *P. kiwiensis.* However, there are exclusive meristic characters (6 pelvic-fin rays is otherwise unknown in the *meteori* species group) as well as presence of preopercular serrations as distinguishing features.

Etymology.—The name *ovatus* is a Latin adjective meaning oval, referring to the general body shape.

Polyipnus ruggeri Baird, 1971
Figure 26

Polyipnus ruggeri Baird, 1971: 102–103 (fig. 78).—Paxton et al., 1989: 192.—Harold, 1990a, 1990b (photophores).—Aizawa, 1990: 97.

Type Material.—Holotype: NMNZ (DMNZ) 4670 (1, 46.8 mm) (not seen).

Other Material.—AMS I.20066 (1, 49.1 mm). AMS I.27166 (1, 65.5 mm). AMS I.21372 (1, 27.1 mm). AMS I.20312 (1, 22.4 mm). USNM 298919 (1, 16.3 mm). ZMUC P207118 (1, 50.3 mm).

Diagnosis.—Autapomorphies: Dorsal lamellar processes of parasphenoid for articulation with basisphenoid absent. Posttemporal spine triangular and dorsally concave. Longitudinal parietal keel continuous, without anterior disjunction and spine. Lateral pigment bar reduced to a slight undulation of ventral margin of dorsal pigment. OVB photophores in a horizontal line or with #1 and #3 slightly elevated. Other characters, in combination: Gill rakers 17 or 18. Abrupt archlike deflection of dorsum pigment ventral margin dorsal to ACA photophores. One short posttemporal spine present. Anal-fin pterygiophore spines and photophore scale denticles absent. ACA photophores separate, #2 and #3 conspicuously elevated relative to first ACB. ACB 8/9. Teeth present on posteromedian vomerine process.

Description.—Moderate to large adult size, largest specimen examined 65.5 mm SL. D (12) 12. A (17) 16–18. P (15) 14–15. V 6–7. GR 5 + 12/13 = (18) 17–18. Vertebrae (33).

Ventral margins of photophore scales smooth, without denticles. OVB 1 + 1 + 1, in a horizontal to anteriorly inclined straight line. AC 1 + 1 + 1, separate, not united in common organ, increasing in elevation incrementally from anterior to posterior. ACA (9, 8–9), with a dorsal step between #3 and #4. ACC (4), compact.

Similar Species.—*Polyipnus ruggeri* most closely resembles *P. meteori* and *P. matsubarai* in some body proportions, meristic character values, pigmentation and posttemporal morphology. Low gill raker counts distinguish this species from *P. matsubarai* (17/18 as compared with 22–24). *P. meteori* differs in its very long lateral pigment bar and elevated first OVB photophore. The near horizontal row of OVB photophores distinguishes *P. ruggeri* from all other members of the genus, except *Polyipnus* sp. B (Last and Harold, MS), a member of the *spinosus* group.

Distribution.—*Polyipnus ruggeri* was originally known only from the eastern Tasman Sea and other New Zealand slope areas but material is reported here which extends its range westward to include the southeast coast of Australia (Fig. 23). This species may occur as deep as 500 m but it has also been taken above 100 m in one night tow (AMS I.20312).

Other species occurring in the region are *P. kiwiensis, P. aquavitus, P. unispinus* and possibly *P. parini.*

Remarks.—*Polyipnus ruggeri* is a member of the monophyletic *P. meteori* species group. Phylogenetic analysis indicates that *P. ruggeri* and *P. meteori* are sister species. One other member of this species group, *P. kiwiensis,* occurs in the Tasman Sea but is relatively basal in the phylogeny of the *meteori* group, as presented here.

Polyipnus ruggeri has three external characters that are unique: reduced lateral pigment bar, OVB photophores nearly in a horizontal line, and convexity of the abdominal profile. The OVB configuration resembles the condition in other sternoptychid genera (e.g., *Argyropelecus, Argyripnus*) but the first and last elements in *P. ruggeri* are dorsal to the second by a very small distance; this situation is not known to occur outside *Polyipnus.* These features of *P. ruggeri* appear to be uniquely derived for this species; being autapomorphies they are of no use in proposing relationships.

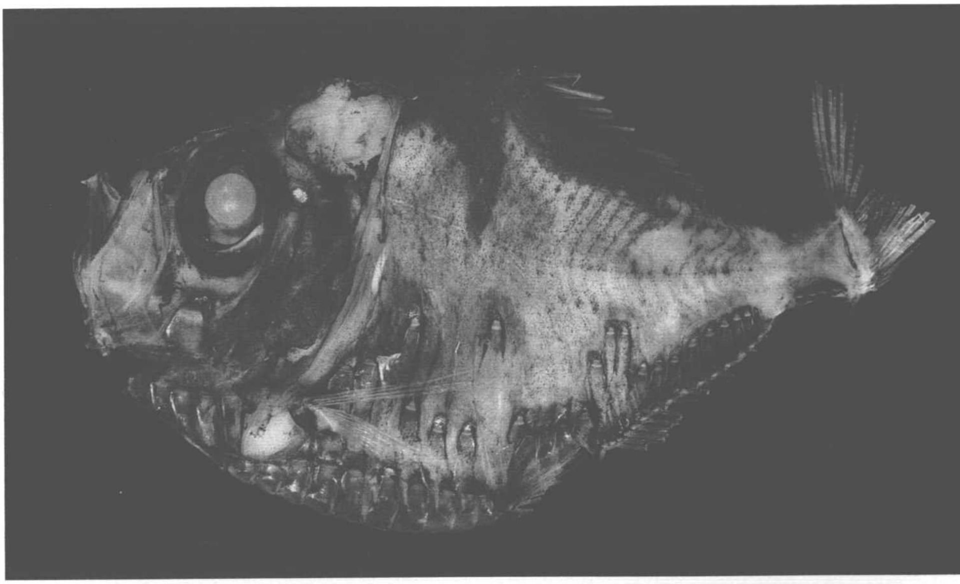

Figure 27. *Polyipnus asteroides*, CAS 61111, 48.6 mm.

Polyipnus asteroides species group

Seven species of the Atlantic Ocean or the Indo-Pacific region: *P. asteroides, P. bruuni, P. clarus, P. laternatus, P. polli, P. surugaensis* and *P. triphanos.*

Polyipnus asteroides Schultz, 1938
Figure 27

(non) *Polyipnus laternatus.*—Jespersen, 1934: 15.
Polyipnus asteroides Schultz, 1938: 138–140 (holotype fig. 44); 1961: 640–641 (part, table 6); 1964: 267, 269–270 (part, holotype fig. 70).—Baird, 1971: 99–101 (part, fig. 76 is *P. clarus*).—Weitzman, 1974: 329–478.—Harold, 1990a: 1114.—Aizawa, 1990: 97.

Type Material.—Holotype: USNM 102979 (1, 39.5 mm). Paratypes: USNM 102978 (4, 26.0–39.5 mm).

Other Material.—CAS 32467 (1, 44.0 mm). CAS 61110 (6, 54.3–64.5 mm). CAS 61111 (3, 42.2–54.9 mm). USNM 295951 (3, 49.4–75.4 mm). USNM 298949 (1, 66.3 mm). USNM 179049 (22, 39.3–66.6 mm). USNM 298940 (10, 66.7–81.3 mm). USNM 203280 (3, 47.2–53.5 mm). USNM 190472 (10, 36.8–50.5 mm). USNM 298945 (1, 61.8 mm). USNM 298936 (3, about 60–75.9 mm). USNM uncat., acc. no. 289062 (5, 70.8–77.8 mm), 11°12'N 74°21'W, (0–) 444 m, OREGON II Sta. 10267, 03 Dec 1968. USNM uncat., acc. no. 261501 (2, 60.6–68.3 mm), 20°42'N 73°38'W, (0–) 666 m, OREGON Sta. 5417, 24 May 1965. USNM uncat., acc. no. 254315 (4, 38.6–61.5 mm), 11°09.5'N 74°24.5'W, (0–) 315–333 m, OREGON Sta. 4838, 16 May 1964. USNM uncat. (2, 40.9–56.2 mm), same data as previous entry.

Diagnosis.—Autapomorphies: Mesopterygoid smooth, without pitting. Gill rakers 20–24. Lateral pigment bar tapered and long, extending ventrally to lateral midline. Overall pigmentation very dark. Anal-fin pterygiophore spine basally expanded. Other characters, in combination: Posttemporal spine single. Photophore scale denticles absent. Second and third ACA photophores united and highly elevated (6.9–7.9% SL) relative to first ACB photophore.

Description.—Maximum adult body size 81.3 mm SL (this study). D (14) 12–16. A (16) 16–17. P (14) 14–15. V 7. GR 7/8 + 13–16 = (24) 20–24.

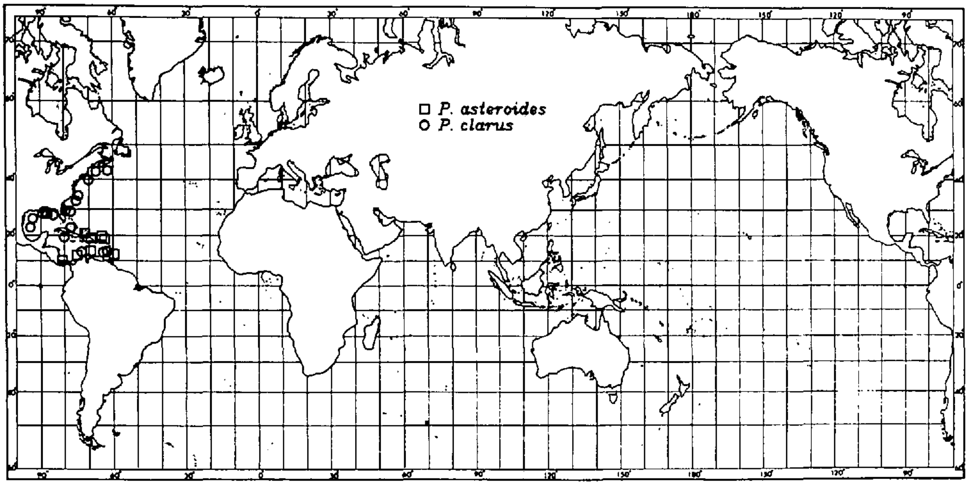

Figure 28. Collection station localities for *P. asteroides* and *P. clarus, P. asteroides* species group.

Ventral margins of photophore scales smooth, without denticles. OVB 1 + 1 + 1, arrangement variable, usually with #2 and #3 at level of posterior VAV photophore and the first dorsally elevated, but occasionally in an anteriorly-inclined straight line. ACA 1 + (2), #1 isolated, located posterodorsally to VAV #5, #2 and #3 posterodorsally to #1 and united in a common organ (ACA #3 elevation relative to ACB #1 6.9–7.9% SL). ACB (9; 8–10), with a conspicuous dorsal step between #3 and #4. ACC (4), compact.

Similar Species.—*Polyipnus asteroides* is most similar to *P. clarus* with regard to photophore patterns and meristic characters. Among features distinguishing *P. asteroides* from *P. clarus* are its deeper body, frequently higher gill raker counts, basally expanded and shorter anal-fin pterygiophore spines, and much darker pigmentation (in preservative) overall. The shape and size of the lateral pigment bar is most similar to that of *P. matsubarai* of the western Pacific, a member of the *meteori* species group.

Distribution.—*Polyipnus asteroides* has been collected through much of the Caribbean Sea in the vicinity of the continental slope of South America and off Puerto Rico (Fig. 28). This species is much more restricted in geographic distribution than the new species *P. clarus* with which it has been confused. Bathymetric records suggest that *P. asteroides* may be a deep-dwelling species, occurring to about 500 or 600 m.

The geographic range of *P. asteroides* overlaps extensively with *P. clarus* (Caribbean Sea) but since they do not appear together in collections they probably occupy different geographic and bathymetric positions within the region. There is also major range overlap with *P. laternatus* in the Caribbean.

Remarks.—The account of *P. asteroides* given by Schultz (1961) included much material here referred to *P. clarus.* Baird (1971) accepted Schultz's treatment and used a specimen of the new species (*P. clarus*) to illustrate *P. asteroides* in his review of the genus. The only published illustration of the species seems to be that of the holotype (Schultz, 1938: fig. 44; 1964: fig. 70).

In addition to the type material listed here, Schultz (1938) designated one other paratype (USNM 96131 [1, 20.0 mm], Lesser Antilles, 0–300 m, GRAMPUS Sta.

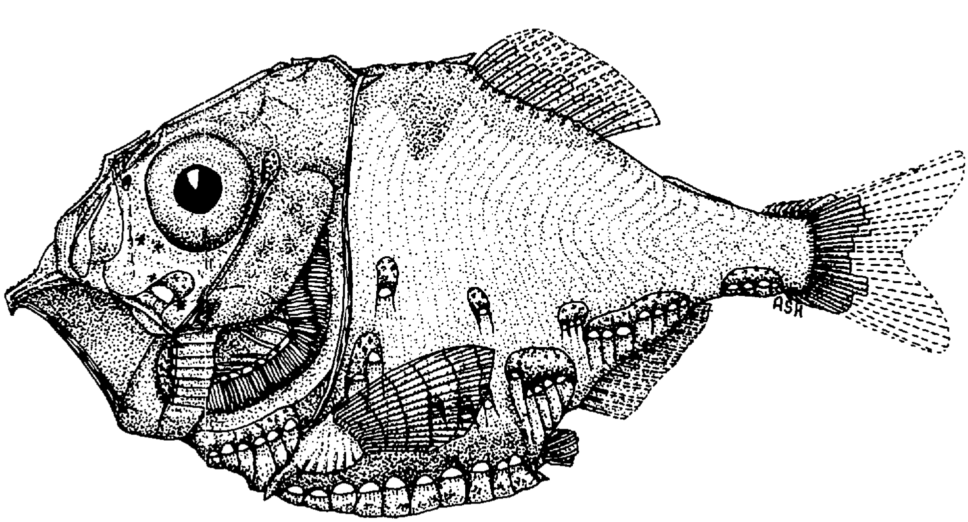

Figure 29. *Polyipnus bruuni*, holotype, USNM 298923, 19.5 mm.

10482, 23 Mar 1917), reportedly in very poor condition. The specimen is no longer listed in the USNM catalog and may be lost.

Polyipnus bruuni new species
Figure 29

Type Material.—Holotype: USNM 298923 (1, 19.5 mm), 02°56'S 40°28'E, 0–240 m, ANTON BRUUN Cr. 8 (International Indian Ocean Expedition), Sta. 421G, 8 Nov 1964.

Diagnosis.—Autapomorphy: ACA (3), in a horizontal line and united in a common organ, highly elevated relative to first ACB. Other characters, in combination: Gill rakers 19. Lateral pigment bar broad, tapered, reaching ventrally about half way to lateral midline. One short posttemporal spine present. Anal-fin pterygiophore spines and photophore scale denticles absent. ACB (7).

Description of Holotype.—Known only from the holotype (19.5 mm SL). D (12). A (15). P (14). V (6). GR (6 + 13) = (19). Vertebrae (13 + 20) = (33). Body profile anterior of dorsal fin and pelvic fin elliptical and deep, tapered posteriorly as far as caudal peduncle at about 30°. Profile of caudal peduncle rectangular, elongate. Margins of dentary and premaxillary bones with minute, recurved teeth. Maxillary with shorter, conical teeth. Four conical palatine teeth. Anterolateral processes of vomer each with a patch of six conical teeth. No teeth present on posteromedian process of vomer. Frontal and parietal keels nonserrate, latter terminating posteriorly in short spine. Posttemporal spine short (3.8% SL). Dorsal limb of posttemporal with two spinelike serrations, ventral limb smooth. Ventral margin of pectoral shield with seven triangular spines. Preopercle with a short (2.1% SL) ventral spine only, embedded within distal lamella of preopercle. Dorsal spinous process short-based, nonserrate, and terminating posteriorly with two acutely triangular posterodorsally-directed spines (one per side). Anal-fin pterygiophore spines absent.

Morphometric characters (% SL): Head length 41.0, orbit length 17.6, body depth 63.9, caudal-peduncle depth 12.4, caudal-peduncle length 18.0, dorsal-fin length 20.5, anal-fin length 22.5, preanal length 74.6, predorsal length 54.9, pre-

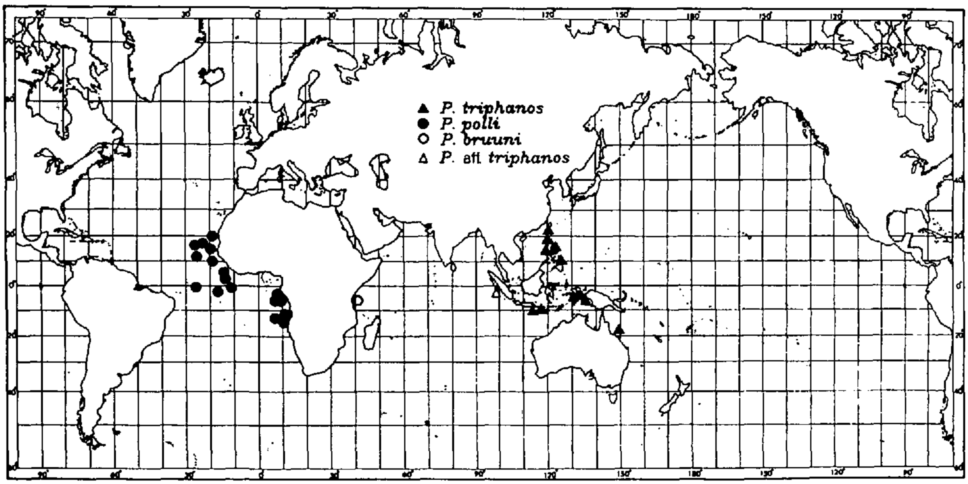

Figure 30. Collection station localities for *P. triphanos, P. polli, P. bruuni,* and *P.* aff. *triphanos, P. asteroides* species group.

ventral length 73.8, postdorsal length 54.1, postanal length 39.3, ACC length 7.8, ACB-C length 5.4.

Ventral margins of photophore scales smooth, without denticles. OVB 1 + 1 + 1, in a "V" configuration. ACA (3), united in a horizontal, linear cluster. ACB (7), with dorsal step between #3 and #4. ACC (4), compact.

Dark pigment saddle with short predorsal notch and short, triangular lateral projection. Postdorsal pigment notch appears to be absent. Dark pigment also present in association with photophore tissues, dorsolateral surface of head, base of dorsal-fin rays, dentary and delineating anterior body-trunk myosepta (epidermis and pigment are missing posteriorly in the holotype).

Similar Species.—*Polyipnus bruuni* is most similar to *P. triphanos,* the only members of the *asteroides* species group lacking anal-fin pterygiophore spines. These two species further differ from other members of the group by the low dorsal-fin ray count (12 or fewer as compared with 13 or more) with the exception of *P. laternatus* which is quite variable (12–15). *Polyipnus bruuni* is distinguished from all other *Polyipnus* species by its unique ACA photophore configuration (3 united).

Distribution.—The *P. bruuni* holotype was collected by open tow to 240 m in the equatorial western Indian Ocean (Fig. 30). The collection label reads "off Madagascar" but the geographical position given is actually more than 10 latitude degrees north of Madagascar and immediately off the coast of Kenya (Somali Basin margin).

The western Indian Ocean has not been well-sampled in the continental slope areas where *Polyipnus* species are most likely to be encountered. *Polyipnus indicus, P. omphus,* and *P. meteori* are the only other species known to occur in the region.

Remarks.—Although the holotype of *P. bruuni* is very small (19.5 mm SL) it appears to have most features that are characteristic of adults of other closely-related species. I suspect that the slightly low ACB photophore count (7), however, reflects an early developmental stage. Photophores of that cluster usually

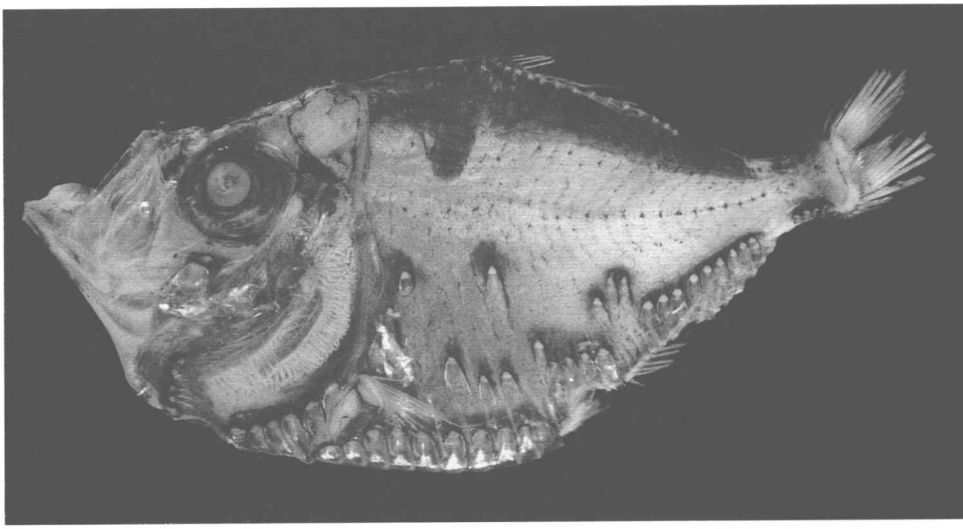

Figure 31. *Polyipnus clarus,* holotype, USNM 273283, 43.6 mm.

appear at body sizes of up to 25 mm SL (Harold, 1990b). There are also potential difficulties in making critical morphometric comparisons between the *P. bruuni* holotype and larger individuals of other species because of allometry. The species can be diagnosed, however, on the basis of a qualitative character; no other species has three united ACA photophores.

Etymology.—Named for the vessel ANTON BRUUN, from which the holotype was collected during the International Indian Ocean Expeditions.

Polyipnus clarus new species
Figure 31

Polyipnus laternatus.—Jespersen, 1934: 15.—Fowler, 1936: 1206–1207 (part).
Polyipnus asteroides.—Schultz, 1961: 621, 640–641 (part); 1964: 267, 269–270 (part, fig. 70 is *P. asteroides* holotype).—Scott, 1965: 1303–1305 (fig. 1).—Baird, 1971: 99–101 (part, fig. 76 only).—Musick, 1973: 173.—Markle et al., 1980: 52.—Scott and Scott, 1988: 172 (unnumbered illustration).—Harold, 1990b: 515.
Polyipnus sp. A.—Harold and Clark, 1992.

Type Material.—Holotype: USNM 273283 (1, 43.6 mm), 33°59′N 76°05′W, 0–409 m, OREGON II, Cr. 9, Sta. 11761, 1 Feb 1972. Paratypes: AMNH 76178 (10, 38.5–54.4 mm), 33°59′N 76°05′W, OREGON II Sta. 11761, 01 Feb 1972. FMNH 66633 (1, 25.4 mm), 29°04′N 87°37′W, OREGON Sta. 3258, 28 Apr 1961. MCZ 66694 (2, 24.7–27.1 mm), 22°22′N 95°20′W, 385–435 m, CHAIN, Cr. 60, 18 Jun 1966. USNM 304745 (18, 31.3–45.7 mm), same data as holotype. ZMUC uncat. (1, 25.9 mm), 13°47′N 61°26′W, 2,500 mwo, DANA Sta. 1183 III.

Other Material.—AMNH 37337 (1, 23.8 mm). AMNH 37336 (1, 27.0 mm). CAS 18718 (1, 22.0 mm). MCZ 40581 (1, 21.6 mm). MCZ 42291 (1, 32.6 mm). MCZ 66694 (2, 28 mm). MCZ 66695 (1, 41.9 mm). MCZ 66696 (2, 26.0–30.9 mm). MCZ 66698 (1, 38.6 mm). MCZ 76365 (2, 33–42 mm). MCZ 90565 (1, 44 mm). MCZ 90566 (4, 39.8–46.6 mm). MCZ 90567 (1, 43.8 mm). MCZ 90568 (1, 39.5 mm). MCZ 90569 (1, 34 mm). MCZ 90570 (1, 37 mm). MCZ 90571 (4, 16–22 mm). MCZ 90572 (3, 18–20 mm). MCZ 90577 (1, 34 mm). MCZ 90578 (1, 25 mm). MCZ 91596 (3, 19–34 mm). MCZ 91615 (1, 37 mm). MCZ 91623 (8, 24–28 mm). MCZ 92650 (3, 23–27 mm). MCZ 92651 (1, 27 mm). MCZ 92652 (1, 42 mm). MCZ 92653 (1, 31 mm). MCZ 92655 (3, 30–56 mm). MCZ 92656 (5, 15–34 mm). MCZ 92657 (3, 29–36 mm). MCZ 92658 (1, 17 mm). MCZ 92659 (2, 17–18 mm). MCZ 92260 (1, 20 mm). MCZ 94478 (4, 15–40 mm). MCZ 94480 (1, 32 mm). MCZ 94496 (6, 20–26 mm). MCZ 97210 (1, 29 mm). MCZ 97211 (1, 32 mm). CAS (SU) 17430 (3, 37.3–

40.8 mm). ROM uncat. (3, 23.3–41.2 mm), 34°25'00"N 75°39'45"W, 0–348 m, 14 Feb 1969. SIO 70-365 (7, 12.0–15.2 mm). USNM 298941 (39, 30.2–46.5 mm). USNM 261627 (6, 34.4–50.3 mm). USNM 302437 (2, 26.2–27.5 mm). USNM 302436 (2, 23.5–27.3 mm). USNM 186016 (5, 28.5–31.4 mm). USNM 190468 (1, 22.6 mm). USNM 186022 (3, 36.1–48.5 mm). USNM 298946 (1, 54.9 mm). USNM uncat. (1, 23.0 mm), 27°42'N 94°26'W, (0–) 370 m, OREGON II Cr. 89, Sta. 4616, 20 Jan 1964. USNM uncat., acc. no. 254315 (6, 21.8–42.7 mm), 27°46'N 94°13'W, (0–) 370 m, OREGON Sta. 4614, 20 Jan 1964. USNM uncat., acc. no. 261501 (1, 40.3 mm), 28°58.5'N 79°57.0'W, (0–) 407–416 m, OREGON Sta. 5250, 19 Feb 1965. USNM uncat., acc. no. 225026 (4, 37.0–44.1 mm), 27°03'N 96°16'W, (0–) 389 m, OREGON Sta. 1093, 04 Jun 1954. USNM uncat., acc. no. 261501 (3, 32.5–37.5 mm), 29°04.5'N 80°01.0'W, OREGON Sta. 5259, 17 Feb 1965. USNM uncat., acc. no. 261501 (1, 37.9 mm), 29°34'N 79°57'W, (0–) 648 m, OREGON Sta. 5748, 19 Nov 1965.

Diagnosis.—Autapomorphies: Maxillary postpalatinad facet reduced, median palatomaxillary ligament attaching to dorsomedial surface of maxilla. Median crest of dorsal spinous process dorsoventrally depressed. Other characters, in combination: Gill rakers 19–21. Lateral pigment bar triangular and short, extending ventrally about half way to lateral midline. Overall pigmentation very pale. Posttemporal spine single. Anal-fin pterygiophore spines long and needlelike, not noticeably expanded basally. Photophore scale denticles absent. Second and third ACA photophores united and highly elevated (4.9–6.6% SL) relative to first ACB photophore. Mesopterygoid pitted over central lateral surface.

Description.—Maximum adult body size 60 mm SL. D (15) 15–16. A (16) 16–17. P (14) 13–15. V 7. GR 5–7 + 13–15 = (21) 19–21. Vertebrae (32) 32/33. Body profile anterior of dorsal fin broadly elliptical, abruptly tapered posteriorly as far as caudal peduncle. Profile of caudal peduncle rectangular, elongate. Margins of dentary, premaxillary and maxillary bones with minute, recurved teeth. One longitudinal row of five or six conical teeth on palatine. Anterolateral processes of vomer each with patch of four or five conical teeth. No teeth present on posteromedian process of vomer. Frontal and parietal keels serrate. Posttemporal spine short (2.4–3.1% SL), dorsally-curved, with minute posteriorly-directed barb on its anterodorsal surface. Ventral margin of pectoral shield bears 6–9 conical spines. Vertical ramus of preopercle smooth, nonserrate, anteroventral ramus with four or five serrations. Preopercle with two spines: ventral spine straight, short (0.9–2.2% SL), except for terminus embedded entirely within distal lamella, and directed ventrally; dorsal spine minute (slightly longer than one preopercular serration). Dorsal spinous process smooth or with one serration on anterodorsal surface, and with two triangular spines, one per side, directed dorsolaterally. First anal-fin pterygiophore bears two long (1.1–2.0% SL), needlelike spines (one per side), ventrolaterally-directed.

Morphometric characters (% SL): Head length 28.6–34.4, orbit length 13.4–16.1, body depth 58.1–64.9, caudal-peduncle depth 9.6–11.2, caudal-peduncle length 12.2–15.4, dorsal-fin length 26.0–28.7, anal-fin length 28.0–29.0, preanal length 72.3–78.9, predorsal length 50.0–52.8, preventral length 68.1–77.1, postdorsal length 50.4–53.1, postanal length 40.1–44.7, ACC length 5.5–6.5, ACB-C length 4.1–5.2.

Ventral margins of all photophore scales smooth, without denticles. OVB 1 + 1 + 1, arrangement variable but usually with #2 and #3 at level of posterior VAV photophore and the first dorsally elevated. ACA 1 + (2), #1 isolated, located posterodorsally to VAV #5, ACA #2 and #3 posterodorsally to #1 and united in common organ. ACB (10/9; 8–10), with dorsal step in arrangement between #3 and #4. ACC (4), compact.

General pigmentation pale brown in preservative. Pigment saddle, ventrally, with a predorsal notch and a short, triangular lateral projection extending about half way to lateral midline.

Similar Species.—Five species have the distinctive ACA photophore arrangement 1 + (2). Of these, *P. clarus* and *P. asteroides* are quite similar and are distinguished on the basis of pigmentation, relative body depth, size and shape of the anal-fin pterygiophore spine, and gill raker counts. Another distinguishing character is the relative distance between the posterior ACA and the anterior ACB photophores which is 4.9–6.6% SL in *P. clarus* as compared with 6.9–7.9% SL in *P. asteroides*. *Polyipnus polli* is distinguished from *P. clarus* by its posteriorly placed dorsal fin, higher dorsal-fin ray and gill raker counts, and unique sinusoidal anal-fin base. *Polyipnus laternatus* has much longer posttemporal spines (5.7–8.6% SL) than any of the aforementioned species (1.7–3.8% SL total range). In contrast to *P. clarus*, *P. triphanos* has low gill raker counts and lacks anal-fin pterygiophore spines.

Distribution.—*Polyipnus clarus* has been collected through much of the Gulf of Mexico and the Caribbean Sea, in the Gulf Stream as far north as the Scotian Shelf (Scott, 1965: "*P. asteroides*" = *P. clarus*) and in the Gulf of Maine (Fig. 28). Bathymetrically, *P. clarus* is most common between 300 and 400 m, according to the various types of gear. The species has been collected by bottom trawl to 833 m but this record may result from fishing off the bottom. There is one record of a capture by midwater trawl at a maximum depth of 39 m—time of day for this sample is not known.

The geographic range of *P. clarus* overlaps with that of *P. asteroides* in the Caribbean Sea. The collections examined in this study suggest that the two species probably occur at different depths. There are no known records of these two species being caught in the same tow. There is also range overlap between *P. clarus* and *P. laternatus* which also occurs through the Caribbean and Gulf of Mexico.

Remarks.—*P. clarus* populations were considered conspecific with *P. asteroides* by previous investigators. In fact, intraspecific variation other than typical dispersion of meristic characters for *P. asteroides* sensu lato has never been reported. Specimens of the new species were the basis of illustrations of *P. asteroides* in Schultz (1961: fig. 16) and Baird (1971: fig. 76), the two most recent revisions, and consequently problems in routine identification have not been encountered. Moreover, the original species *P. asteroides* of Schultz (1938) is highly restricted in geographical distribution (Caribbean Sea, Greater Antilles) and has been caught on very few occasions. Detailed studies of pigmentation pattern, morphometric characters and micromorphology show that these are separate and quite distinct species.

Etymology.—The name *clarus* is a Latin adjective meaning bright or distinct, referring to the very light pigmentation of *P. clarus* in comparison to *P. asteroides* with which it has been confused.

Polyipnus laternatus Garman, 1899
Figure 32

Polyipnus laternatus Garman, 1899: 238.—Norman, 1930: 305 (part, fig. 14 is *P. polli*).—Fowler, 1936: 1206–1207 (part).—Parr, 1937: 55 (fig. 22).—Schultz, 1938: 142–143; 1961: 639; 1964: 267, 270–271 (fig. 71).—Baird, 1971: 92–94 (fig. 70).—Weitzman, 1974: 344 (fig. 10).—Harold, 1990a: 1114; 1990b: 515.
(non) *Polyipnus spinosus*.—Brauer, 1906: 121 (part).—Rivero, 1936: 56.

Type Material.—Holotype: MCZ 27945 (1, 37.6 mm).

Other Material.—MCZ 40570 (1, 35.0 mm). MCZ 40571 (1, 21.0 mm). MCZ 40572 (3, 31.7–34.5

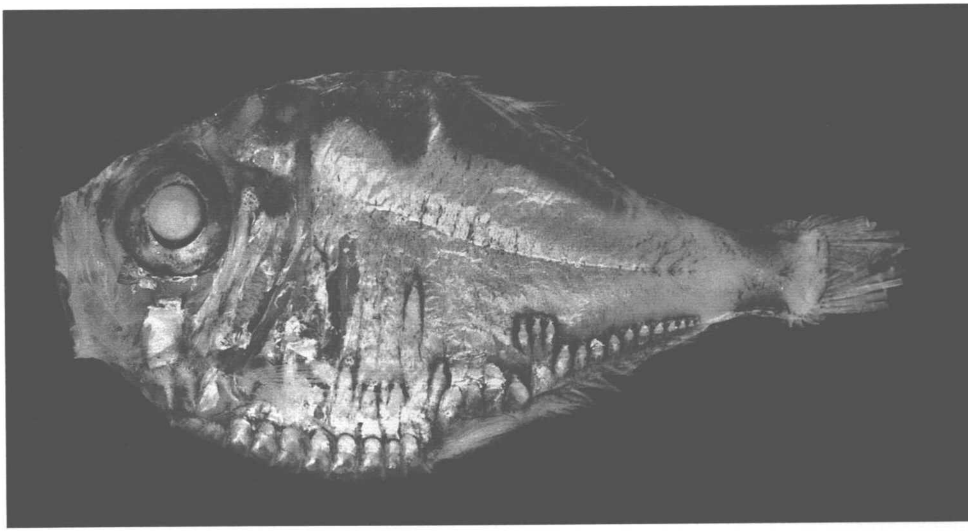

Figure 32. *Polyipnus laternatus*, MCZ 40575, 31.1 mm.

mm). MCZ 50573 (2, 34.4–34.6 mm). MCZ 40574 (1, 40.1 mm). MCZ 40575 (2, 31.1–33.0 mm). MCZ 40576 (14, 18.7–22.0 mm). MCZ 40577 (1, 26.2 mm). MCZ 40578 (1, 34.2 mm). MCZ 40579 (2, 20.9–23.0 mm). MCZ 40580 (1, 23.0 mm). MCZ 40582 (1, 34.0 mm). USNM 17950 (17, 29.6–36.7 mm). USNM 298237 (2, 38.5–44.0 mm). USNM 298924 (12, 32.4–43.9 mm). USNM uncat. (1, 41.5 mm), 20°42′N 73°38′W, (0–) 666 m, OREGON Sta. 5417, 24 May 1965.

Diagnosis.—Autapomorphies: Indistinct dorsal step between ACB photophores #3 and #4. Ten or more ACB photophores. Iliac spine short, its length less than that of ischial process. Ventral preopercular spine largely embedded in distal lamella with tip as a free spine. Other characters, in combination: Gill rakers 16–19. Lateral pigment bar short, tapered, reaching about half way to lateral midline. Posttemporal spine single, length moderate (5.7–8.6% SL). Anal-fin pterygiophore spines long, needle-like. Photophore scale denticles absent. ACA photophores 1 + (2) or 1 + 1 + 1, #2 and #3 elevated relative to #1. ACB 11–13.

Description.—Body size relatively small, largest examined 43.9 mm SL. D (15) 12–15. A (15) 15–18. P 12–14. V 6–7. GR 4–6 + 11–14 = (18) 16–19. Vertebrae (34) 32–33.

Ventral margins of all photophore scales smooth, without denticles. OVB 1 + 1 + 1, in a shallow "V" configuration. ACA 1 + (2), rarely 1 + 1 + 1, all in close proximity but #1 positioned ventrally of #2 by distance equal to its diameter, #3 highly elevated relative to ACB #1. ACB (11; 11–13), with slight dorsal step between #3 and #4. ACC (4), compact.

Similar Species.—*Polyipnus laternatus, P. clarus, P. asteroides, P. polli, P. omphus, P. unispinus,* and *P. aquavitus* are the only members of the genus with first anal-fin pterygiophore spines. These spines are useful in identification, being visible in specimens as small as 10 mm SL. *Polyipnus laternatus* is distinguished from *P. clarus, P. asteroides* and *P. polli* by higher ACB photophore counts (11–13 compared with a total range of 7–10 for the other three species) and longer posttemporal spines. *Polyipnus laternatus* is separated from *P. unispinus* and *P. aquavitus* (both of the *omphus* species group) on the basis of its higher gill raker counts (16–22 as compared with 11–12 and 13–15, resp.) and highly elevated

ACA photophores. With regard to body shape, ACB photophore number and configuration, and posttemporal spine morphology *P. laternatus* is most similar to *P. omphus*; *P. laternatus* is distinguished by its elevated ACA photophores with #2 and #3 usually united, OVB photophores in a "V" configuration as opposed to an anteriorly-inclined straight line, and ACB photophores 11–13 compared with 10–12.

Distribution.—*Polyipnus laternatus* has been collected throughout the Caribbean Sea (type locality off Barbados) and Gulf of Mexico with some captures in the Gulf Stream as far north as Cape Hatteras (Fig. 35). Few data on vertical distribution are available. Schultz (1964: 271) gives a bathymetric range of 240 to 1,200 fm (about 444–2,220 m) but these figures were presumably derived from the maximum depth fished by open tows. Collections examined in the present study indicate a range of about 370 to 500 m.

The geographic range of *P. laternatus* overlaps to a large extent with that of *P. asteroides* and *P. clarus* but data are insufficient to detect any interspecific differences in bathymetric range. In one instance *P. laternatus* and *P. asteroides* were collected in the same tow (depth 0–666 m, USNM uncat., OREGON Sta. 5417) but there is no way of determining at which depths the specimens were taken.

Remarks.—Baird (1971) delimited the *P. laternatus* species complex, consisting additionally of *P. omphus, P. unispinus* and *P. aquavitus. Polyipnus danae* was tentatively ascribed to this group on the basis of such features as elongate posttemporal spines and high ACB photophore counts (Harold, 1990a). The phylogenetic analysis supports the hypothesis that *P. laternatus* is related to the other members of the *P. asteroides* species group and not to the aforementioned. Considerable homoplasy was encountered but placement of *P. laternatus* in the *asteroides* group is parsimonious and therefore preferred to other hypotheses.

According to the specimens examined, the range for total gill raker count is 16 to 19 with 18 in the holotype. Schultz (1961) reported a range of 18 to 22 which was based on more material. The entire observed plus reported range is given here but until some of the higher values are verified they should not be used as key characters. I also draw attention to MCZ 40576 which was listed as representative of *P. asteroides* (sensu lato) by Schultz (1961).

Polyipnus polli Schultz, 1961
Figure 33

Polyipnus laternatus.—Norman, 1930: 305 (fig. 14).—Fraser-Brunner, 1931: 218.—Fowler, 1936: 1206–1207 (part).—Poll, 1953: 65.—Marshall, 1960: 22.

Polyipnus polli Schultz, 1961: 635 (holotype fig. 13); 1964: 267, 271–272 (fig. 72).—Baird, 1971: 98–99; 1986: 257–258 (fig. 75.10).—Ahlstrom et al. 1984: 184–198 (photophore development, table 52, fig. 104).—Harold, 1990a: 1114.—Aizawa, 1990: 97.

Type Material.—Holotype: MRAC 95092 (1, 22.0 mm) (not seen). Paratype: USNM 179878 (1, 26.0 mm).

Other Material.—BMNH 1930.1.12.458–467 (10, 16.0–33.0 mm). BMNH uncat. (3, 10.6–12.0 mm), 05°54'S 11°19'E, R.R.S. DISCOVERY Sta. 276. MCZ 41581 (1, 17.5 mm). MCZ 66699 (5, 15.0–25.6 mm). MCZ 66700 (2, 18.2–21.1 mm). MCZ uncat. (27, 11.4–30.5 mm), 16°22'N 21°43'W to 16°23'N 21°50'W, (0–) 230–250 (–0) m, ATLANTIS II Cr. 59, field no. RHB 2062, 0255–0450 h, 15 Nov 1970. MCZ uncat. (3, 30.8–40.2 mm), 12°51'S 08°15'E to 12°47'S 08°22'E, (0–) 390–400 (–0) m, ATLANTIS II Cr. 60, field no. RHB 2279, 2020–2300 h, 03 Jun 1971. MNHN 1962–733 (1, 16.8 mm). MNHN 1962-725 (1, 17.5 mm). MNHN 1962–722 (1, 37.2 mm). ZMUC P206955 (6, 25.4–32.1 mm). ZMUC uncat. (2, 30.1–34.5 mm), 17°55'N 24°55'W, 1,000 mwo, DANA Sta. 1159. ZMUC uncat. (4, 4.0–33.0 mm), 18°22'N 18°14'W, 1,000 mwo, DANA Sta. 4007 I, 0315–0515 h, 15 Mar 1930. ZMUC uncat.

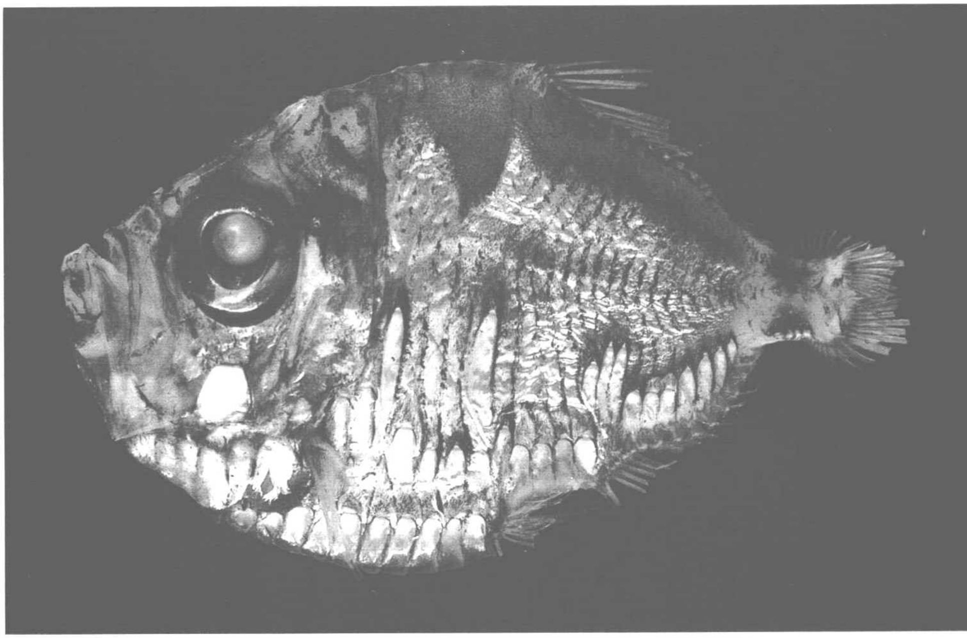

Figure 33. *Polyipnus polli*, ZMUC uncat., DANA Sta. 1159, 30.1 mm.

(6, 19.0–25.0 mm), 00°31′S 11°02′W, 1,000 mwo, DANA Sta. 4000 I, 0230–0430 h, 04 Mar 1930. ZMUC uncat. (3, 9.0–13.0 mm), 18°22′N 18°14′W, 1,000 mwo, DANA Sta. 4007 XI, 0700–0900 h, 15 Mar 1930. ZMUC uncat. (1, 15.0 mm), 08°26′N 15°11′W, 600 mwo, DANA Sta. 4003 VIII, 1845–2045 h, 09 Mar 1930.

Diagnosis.—Autapomorphies: Longitudinal blades of pectoral fin radials reduced. Anal-fin base sinusoidal, highly convex posteriorly. Other characters, in combination: Gill rakers 20–23. Lateral pigment bar triangular and short, extending ventrally about half way to lateral midline. Posttemporal spine single. Anal-fin pterygiophore spines long and needlelike. Second and third ACA photophores united and highly elevated (6.9–7.9% SL) relative to first ACB. ACB (7–8).

Description.—Maximum adult body size moderate, not exceeding 50 mm SL. D (16) 14–16. A (15) 15–17. P (13) 13–14. V 7. GR 6/7 + 14–16 = (20) 20–23.

Ventral margins of all photophore scales smooth, without denticles. OVB 1 + 1 + 1, usually in a "V" configuration but with #1 elevated slightly with respect to #3. ACA 1 + (2), #1 isolated, located posterodorsally to VAV #5, #2 and #3 posterodorsally to #1 and united in common organ. ACB (7; 7–8), with conspicuous dorsal step between #3 and #4. ACC (4), compact. According to Ahlstrom et al. (1984), some photophores of the BR, OP and PV groups are present in individuals as small as 4.3 mm SL [SL or NL?], with the full complement of all groups in place by about 23.5 mm SL. Development of ACA and ACB photophores is more protracted than in any other photophore group.

Similar Species.—*Polyipnus polli* is most similar to *P. asteroides*, *P. clarus* and *P. laternatus*, the four members of the *asteroides* species group with anal-fin pterygiophore spines. Of these species *P. clarus* is most similar to *P. polli*, both having short triangular lateral pigment bars and long, needlelike anal-fin pterygiophore spines. *Polyipnus polli* is distinguished from *P. clarus* by the posterior

position of the dorsal fin (predorsal length 55.1–63.5 as compared with 50.0–52.8% SL, respectively) and from all other *Polyipnus* species by the unique sinusoidal anal-fin base.

Distribution.—*Polyipnus polli* is restricted to the eastern tropical to subtropical Atlantic Ocean from the Gulf of Guinea and Benguelan Upwelling region northwards to the Mauritanian Upwelling region (Fig. 30). The species has been captured above 200 m depth at night.

Remarks.—In the original description Schultz (1961: 636, table 6) indicates that one third of the type specimens have six and the remaining have seven ACB photophores. The size range of the series is 17.0–26.0 mm SL and from ontogenetic studies of these photophores (Harold, 1990b) it is likely that one or two more photophores would have developed. According to the material examined in the present study a count of 6 ACB photophores would only be expected in juveniles or subadults of *P. polli.*

Polyipnus surugaensis Aizawa, 1990

Polyipnus surugaensis Aizawa, 1990: 95–97 (holotype figs. 1 and 2).

Type Material.—Holotype: NSMT P21480 (1, 37.1 mm).

Diagnosis.—Autapomorphies: First two OVB photophores at same level, third elevated, at level of first VAV. Predorsal pigment notch elongate, reaching dorsally to dorsal fin origin. Other characters, in combination: gill rakers 17, anal fin rays 17, ACB photophores 9, anal-fin pterygiophore spines absent, no teeth on posteromedian process of vomer.

Description.—Only known specimen, 37.1 mm SL. D (12). A (17). P (13). V (7). GR (7 + 10 = 17). Vertebrae (32).

Ventral margins of all photophore scales smooth, without denticles. OVB 1 + 1 + 1, #1 and #2 at same level, #3 elevated to level of VAV #1. ACA 1 + (2), #1 isolated, located posterodorsally to VAV #5, #2 and #3 united in common organ and highly elevated relative to first ACA. ACB (9), with dorsal step between #3 and #4. ACC (4), compact.

Similar Species.—In general body form and the derived ACA configuration *P. surugaensis* resembles other members of the *asteroides* group. Of these species only *P. surugaensis, P. triphanos,* and *P. bruuni* lack anal-fin pterygiophore spines. The meristic values do not distinguish *surugaensis* and *triphanos,* leaving only the unique OVB configuration and pigmentation of the former as reliable diagnostic characters. Members of the *meteori* group are also similar to *surugaensis*; the lack of teeth on the posterior process of the vomer readily distinguishes *surugaensis.*

Distribution.—Known from a single collection from Suruga Bay.

Remarks.—Aizawa (1990) distinguished *P. surugaensis* from *P. triphanos* on the basis of published meristic character values for the type series reported by Schultz (1938). In the present treatment, the latter is viewed as a highly variable species, some of the specimens examined being very similar to *P. surugaensis* in fin ray counts and dorsal pigmentation.

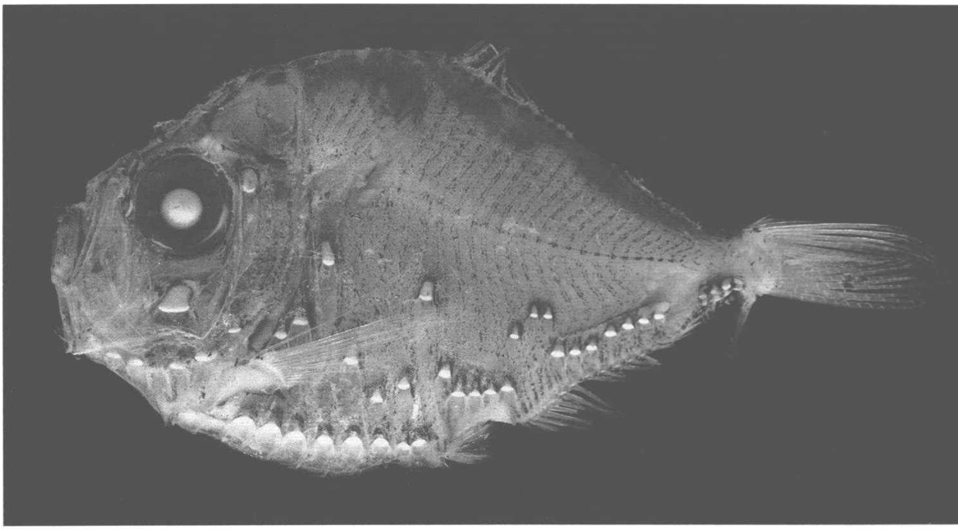

Figure 34. *Polyipnus triphanos*, CAS 34899, 40.4 mm.

Polyipnus triphanos Schultz, 1938 complex
Figure 34

Polyipnus triphanos Schultz, 1938: 140 (holotype fig. 45); 1961: 140 (holotype fig. 15).—Baird, 1971: 97–98 (fig. 74, reproduction of Schultz, 1938: fig. 45).—Fujii, 1984: 47 (pl. 49).—Harold, 1990a: 1114; 1990b: 515.—Aizawa, 1990: 96–97 (fig. 2B, pigmentation pattern).

Type Material.—Holotype: USNM 103027 (1, 20.4 mm). Paratypes: USNM 103028 (2, 17.6–21.0 mm).

Other Material.—AMS I.25816-008 (1, 40.3 mm). AMS I.24316-004 (1, 43.8 mm). AMS I.24338-001 (1, 47.3 mm). CAS 56034 (10, 17.9–30.6 mm). CAS 34899 (1, 40.4 mm). IOAN uncat. (1, 39.0 mm), 01°43′S 143°04′E, 0–500 m, VITYAZ Cr. 50, Sta. 7321, 6 Apr 1975. IOAN uncat. (1, 29.3 mm), 05°37′S 130°50′S to 05°36′S 130°51′E, 100–0 m, VITYAZ Cr. 57, Sta. 7263, 2315–0000 h, 19–20 Mar 1975. SIO 77-167 (1, 37.5 mm). SIO 77-184 (1, 26.8 mm). ZMUC P206962 (1, 28.9 mm). ZMUC P206963 (2, 26.5–30.4 mm). ZMUC uncat. (1, 24.8 mm), 01°19′S 100°12′E, 500 mwo, DANA Sta. 3881 I, 2345–0145 h, 29 Oct 1929.

Diagnosis.—Autapomorphies: Anteriormost branchiostegal ray of posterior ceratohyal narrow, not expanded. Photophore OVB #1 highly elevated relative to other OVB. Other characters, in combination: Gill rakers 14–19. One short posttemporal spine present. Anal-fin pterygiophore spines and photophore scale denticles absent. ACA 1 + (2), second and third photophores united and highly elevated relative to first ACA and ACB. ACB (8–10).

Description.—Small to moderate maximum adult body size, largest examined 47.3 mm SL. D 11–12. A 15–18. P 13–14. V 7. Vertebrae (33). GR 4–6 + 10–13 = (15) 14–19.

Ventral margins of all photophore scales smooth, without denticles. OVB 1 + 1 + 1, in a "V" configuration but with #1 elevated dorsally about diameter of one OVB photophore in relation to #3. ACA 1 + (2), #1 isolated, located posterodorsally to VAV #5, #2 and #3 united in common organ and highly elevated relative to first ACA and ACB. ACB (8/9; 8–10), with dorsal step between #3 and #4. ACC (4), compact.

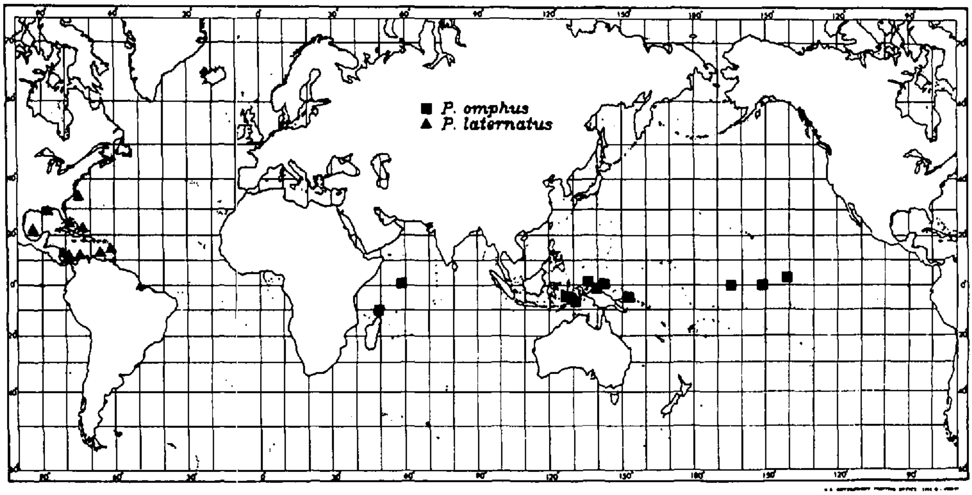

Figure 35. Collection station localities for *P. omphus* (*P. omphus* species group) and *P. laternatus* (*P. asteroides* species group).

Similar Species.—*Polyipnus triphanos* is most similar to *P. asteroides, P. clarus, P. laternatus, P. polli* and *P. surugaensis.* These species all have the 1 + (2) ACA photophore arrangement which, except for *P. bruuni* with ACA (3), is characteristic of the *P. asteroides* species group. Some specimens of *P. kiwiensis* have the posterior two ACA photophores in very close proximity but they are not joined. Of all the species with 1 + (2) ACA only *P. triphanos* and *P. surugaensis* lack anal-fin pterygiophore spines. These two species also have a broad postdorsal pigment notch. Low gill raker counts further distinguish *P. triphanos* and *P. surugaensis*: 13–18 in *P. triphanos* and 17 in *P. surugaensis* as compared with 20–24, 19–21 and 20–22 in *P. asteroides* and *P. clarus* and *P. polli,* respectively. Gill raker counts overlap with those of *P. laternatus* (16–22) but *P. triphanos* and *P. surugaensis* are together distinguished by low ACB photophore number (7–10 and 9, respectively, vs. 10–13). That these last two species are most similar was noted by Aizawa (1990), the only really clear difference being the OVB photophore configuration. In *P. triphanos* they are in a "V" configuration whereas *P. surugaensis* has the unique condition of the first two at the same height and the third elevated.

Distribution.—*Polyipnus triphanos* occurs around the Philippine Islands and Taiwan in the South China Sea and southward through the Sulu, Celebes and Banda Seas and into the western Coral Sea (one record) (Fig. 30). There are reports of this species from the western Indian Ocean, and the Japanese Archipelago (Fujii, 1984).

Discrete-depth samples taken by Rectangular Midwater Trawl (RMT-8; *Snellius-II*) in the Banda Sea indicate that *P. triphanos* occurs between 100 and 300 m at night. A sample from the Philippines (CAS 34899) shows *P. triphanos* occurring above 250 m during daylight hours. Extensive sampling by *Alpha Helix* in the Banda Sea (Southeast Asian Bioluminescence Expedition, 1975) was negative for *P. triphanos,* although other *Polyipnus* species were taken, suggesting extreme patchiness, migratory behavior, annual life cycle or extreme interannual variation in population size.

Figure 36. *Polyipnus aquavitus,* AMS I.19762-002, 35.3 mm.

Remarks.—*Polyipnus triphanos* is quite variable with regard to a number of meristic, pigmentation and photophore characters. Of special note is variation in the lateral pigment bar, which usually varies very little in *Polyipnus* species. However, from the few samples containing more than one specimen pigmentation patterns appear to be "fixed" within individual *P. triphanos* population samples. There are meristic and dentition characters which also appear to vary geographically. A systematic analysis based on more material may reveal that there are several species divisable from that recognized here as *P. triphanos* complex. One specimen in particular (ZMUC uncat., 24.8 mm, DANA Sta. 3881 I) from the Java Trench is very likely a representative of an undescribed species, but is referred to *P.* aff. *triphanos* pending capture of additional material.

Polyipnus omphus species group

Four species of the Indo-Pacific region: *P. aquavitus, P. danae, P. omphus* and *P. unispinus.*

Polyipnus aquavitus Baird, 1971
Figure 36

Polyipnus aquavitus Baird, 1971: 96–97 (holotype fig. 72).—Weitzman, 1974: 373 (fig. 44B, sagitta).—Schalk, 1988: 31–32.—Paxton et al., 1989: 192.—Harold, 1990a: 1114; 1990b: 515.

Type Material.—Holotype: ZMUC P20969 (1, 34.0 mm). Paratypes: ZMUC P20970–P20981 (11, 15.0–31.0 mm). MCZ 46526 (2, 21.9–31.5 mm).

Other Material.—AMS I.19762-002 (3, 22.3–35.3 mm). AMS I.16494-004 (1, 24.2 mm). AMS I.20316-005 (3, 21.4–36.6 mm). AMS I.19761-029 (10, 11.0–34.4 mm). AMS I.20310-017 (3, 18.6–21.7 mm). AMS I.16492-008 (3, 12.5–15.0 mm). IOAN uncat. (2, 18.8–22.6 mm), 02°36'S 147°35'E, 800–0 m, VITYAZ Cr. 50, Sta. 6437, 14 May 1971. IOAN uncat. (1, 31.2 mm), 05°34'S, 130°48'E, 1,500–0 m, VITYAZ Cr. 57, Sta. 7261, 19 Mar 1975.

Diagnosis.—Autapomorphies: Two epurals, distally fused. Lateral pigment bar short, hemispherical. Other characters, in combination: Gill rakers 13/14. Posttemporal spine single, elongate. Anal-fin pterygiophore spines long, needlelike.

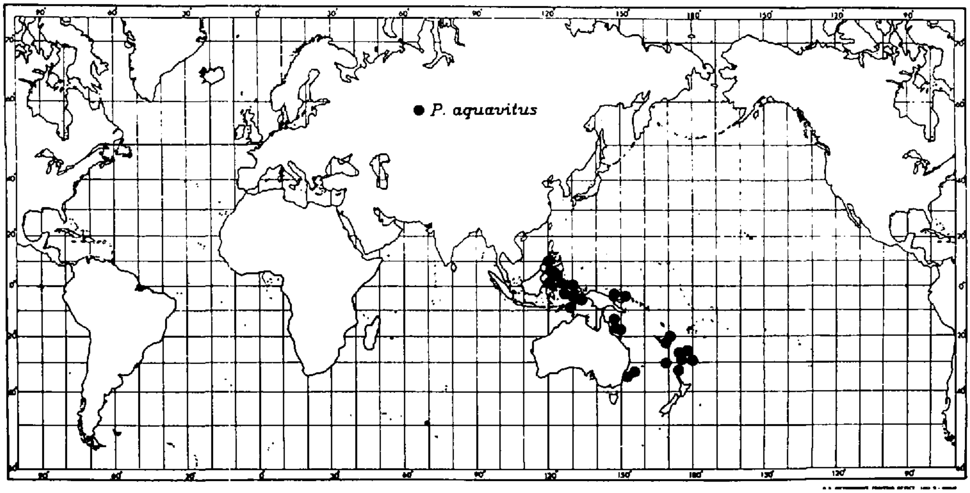

Figure 37. Collection station localities for *P. aquavitus, P. omphus* species group.

Photophore scale denticles absent. ACB photophores (9–11). ACC photophores separated by broad gaps.

Description.—Miniature species, maximum adult body size 35.3 mm SL. D (13) 12–14. A (15) 14–16. P 12–14. V 7. GR 4–5 + 9–10 = (13) 13–15. Vertebrae (35) 31–35.

Ventral margins of all photophore scales smooth, without denticles. OVB 1 + 1 + 1, in an anteriorly-inclined straight line. ACA 1 + 1 + 1, separate (not united in a common organ), in anteriorly-inclined straight line. ACB (10; 9–11). ACC (4), reflectors separated by gaps greater than diameter of one photophore.

Similar Species.—*Polyipnus aquavitus* is most similar to *P. unispinus* and *P. danae,* two other miniature species (standard length less than 40 mm). *Polyipnus aquavitus* is distinguished from both by gill raker counts (13–15 compared with 11/12) and a rectangular as compared with a long, rodlike caudal peduncle. Also see Similar Species for *P. danae.*

Distribution.—*Polyipnus aquavitus* has been collected off the east coast of Australia (Coral and Tasman Seas), New Caledonia, New Hebrides, various sites in the South Fiji Basin, and Indonesia (Celebes, Banda, Halmahera, Sulu Seas) (Fig. 37). This species was thought by Baird (1971) to be disjunct from the Tasman to the Banda Sea but additional collections reported here indicate a broad continuous geographic range.

Polyipnus aquavitus was captured at depths above 50 m at night (Sulu Sea only), but according to other data from discrete-depth sampling (RMT-8 net) the bathymetric range is about 350 to 1,100 m during the day and 90 to 500 m at night. The 1,100 m value was the maximum depth fished by an oblique tow that finished at 450 m. Specimens were also collected by the same gear between 1,000 and 1,400 m but the presence of *P. aquavitus* in the shallower sample which preceded suggests at least a possibility of sample contamination. *Polyipnus aquavitus* has been taken in discrete-depth tows with *P. unispinus* or *P. triphanos* in Indonesia indicating very little or no bathymetric separation between these species in that region.

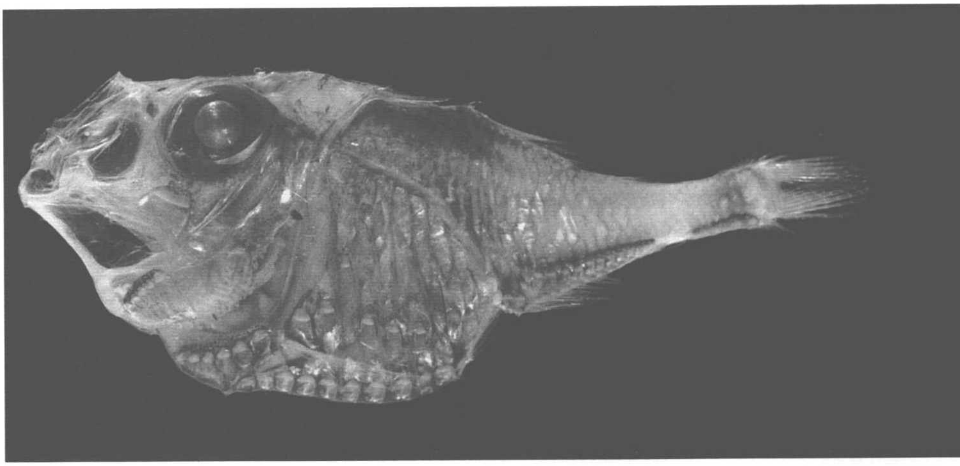

Figure 38. *Polyipnus danae*, paratype, ZMUC P208578, 27.3 mm.

Remarks.—Populations in the seas of Indonesia (e.g., Banda Sea) appear to be characterized by a slightly deeper body. There are, however, no detectable meristic differences among the population samples of *P. aquavitus*. The observed morphometric differences may be a result of differential growth rates, since the Banda Sea is known to be an area of intense upwelling and elevated productivity (van der Spoel and Schalk, 1988) and the Coral and Tasman Seas are not.

Polyipnus danae Harold, 1990
Figure 38

Polyipnus danae Harold, 1990a: 1112–1114 (holotype fig. 1).

Type Material.—Holotype: ZMUC P206919 (1 male, 26.5 mm). Paratypes: ZMUC P206920 (1, 24.2 mm), ZMUC P208577 (1, 24.8 mm), ZMUC P208578 (1, 27.3 mm), ZMUC P208579 (1, 25.4 mm), ZMUC P208580 (1, about 26 mm), ZMUC P208581 (1, about 30 mm).

Diagnosis.—Autapomorphies: Minute, transversely elongate antorbital. Paired expanded lateral flanges of first anal-fin pterygiophore. Extensive separation of dorsal limb of parasphenoid and vertical shaft of basisphenoid. Lateral pigment bar indistinct, triangular. Anal-fin pterygiophore spines and photophore denticles absent. Other characters, in combination: Gill rakers 11/12. Posttemporal spine single, elongate. ACB photophores 11 or 12. ACC photophore reflectors separated by broad gaps. Caudal peduncle highly elongate, rodlike.

Description.—Miniature species, maximum known adult body size 27.5 mm. D (13) 11–13. A (15) 15–18. P (13) 11–13. V (6) 6. GR 3/4 + 8/9 = (11) 11–12. Vertebrae (36).

Ventral margins of photophore scales smooth, without denticles. OVB 1 + 1 + 1, in an anteriorly-inclined straight line. ACA 1 + 1 + 1, separate (not united in common organ), in anteriorly-inclined line. ACB (12; 11–12). ACC (4), reflectors separated by broad gaps (greater than or equal to diameter of one photophore).

Similar Species.—*Polyipnus danae* most closely resembles *P. unispinus* and *P. aquavitus*. These three species have relatively long posttemporal spines (10.5–13.7, 10.5–16.4, 10.1–16.6% SL, respectively) compared with *P. omphus* (5.7–

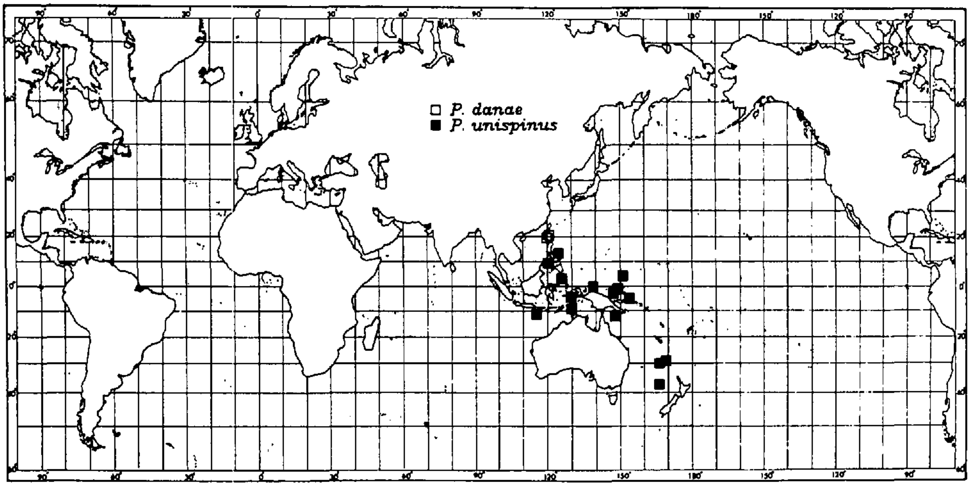

Figure 39. Collection station localities for *P. danae* and *P. unispinus*, *P. omphus* species group.

10.0% SL) and *P. laternatus* (5.7–8.5% SL), two other rather similar species. The *P. danae-P. unispinus-P. aquavitus* group is further characterized by small body size (less than 40 mm SL, and attaining sexual maturity at less than 30 mm), and very low gill raker counts (11–12; 11–12; 13–15, respectively, compared with *P. omphus*, 17–21, and *P. laternatus*, 16–22). *Polyipnus danae* is distinguished from all of the aforementioned by the lack of external anal-fin pterygiophore spines.

Distribution.—*Polyipnus danae* is known only from two collections made off the Philippine Islands in the South China Sea, during the 1928–1930 DANA Expedition (Fig. 39). The specimens were trawled with 2,000 and 1,000 m wire (holotype and paratypes, respectively), indicating that this species occurs at some level between the surface and a maximum depth of about 700 m. The geographic positions of the collecting stations suggest that *P. danae*, like many other *Polyipnus*, may be associated with the continental slope.

The area around the Philippines is particularly rich in *Polyipnus* species but only *P. danae, P. triphanos, P. spinifer, P. ovatus* and *P. meteori* are known from collecting stations within the South China Sea.

Remarks.—The *P. laternatus* complex, consisting of *P. laternatus, P. omphus, P. aquavitus,* and *P. unispinus* was delimited by Baird (1971) on the basis of a single long posttemporal spine in members of each species, a relatively high number of anal (=ACB) photophores, the first supra-anal (=ACA) photophore at the level of the second or dorsally, and elongate body shape. Pending completion of phylogenetic analysis, *P. danae* was provisionally placed by Harold (1990a) in this group. The analysis was shown that of these five species, all except *P. laternatus* together constitute a monophyletic group. A new group, the *P. omphus* species group is recognized here which excludes *P. laternatus.*

In an unpublished report Søgaard (1975) listed the specimens now recognized as *P. danae* as *P. aquavitus.* Although these two species are similar in pigmentation and scale denticulation, *P. danae* is much more similar to *P. unispinus* with which it shares the lowest gill raker counts in the genus (11–12) and a unique rodlike caudal peduncle. *Polyipnus danae* shares an unusual character (reduced

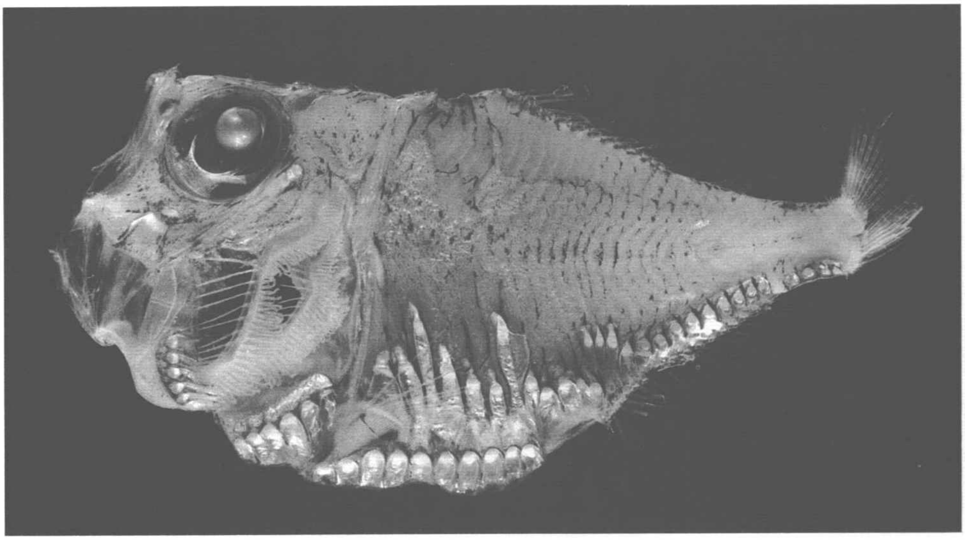

Figure 40. *Polyipnus omphus*, ZMH 4886, 32.9 mm.

anal-fin pterygiophore spines) with many *Polyipnus* species but not with the remaining members of the *P. omphus* species group.

Polyipnus omphus Baird, 1971
Figure 40

(non) *Polyipnus laternatus*.—Kobayashi, 1963: 179.—Kotthaus, 1967: 26 (fig. 41; otoliths, figs. 42 and 43).

Polyipnus omphus Baird, 1971: 94–96 (fig. 71).—Harold, 1990a: 1114; 1990b: 515.

Type Material.—Holotype: BMNH 1970.7.30.1 (1, 43.0 mm). 11°26.8′S (not 11°21′S as reported by Baird, 1971: 94) 48°58.2′E, (0–) 200 m, R.R.S. DISCOVERY Sta. 5509, 21 Aug 1964. Paratype: MCZ 46525 (1, 35.1 mm), same data as holotype.

Other Material.—IOAN uncat. (1, 33.6 mm), 05°14′S 41°51′E, 1,000–0 m, VITYAZ Cr. 31, Sta. 4688, 2054–2145 h, 17 Mar 1960. IOAN uncat. (1, 41.1 mm), 01°15′S 142°46′E, 1,000–0 m, VITYAZ Cr. 57, Sta. 7318, 1975. IOAN uncat. (2, 31.6–35.5 mm), 00°01′S 175°56′W to 00°03′S 176°07′W, 5,428–0 m, VITYAZ Cr. 34, Sta. 5139, 1145–1205 h, 09 Nov 1961. MCZ 64696 (1, 44.3 mm). MCZ 64695 (1, 55.9 mm). SIO 60-236-10 (1, 28.4 mm). SIO 68-534-10 (1, 33.6 mm). USNM 265967 (1, 33.2 mm). ZMH 4886 (2, 18.1–32.9 mm). ZMUC P206932 (1, 19.5 mm). ZMUC P206933 (1, 51.0 mm). ZMUC P206934 (1, 45.3 mm). ZMUC P207116 (1, 40.0 mm).

Diagnosis.—Autapomorphies: Lateral pigment bar broad-based, triangular, reaching about half way to lateral midline; elongate curvilinear lightly pigmented area immediately posterior of projection. ACA photophores 1 + 1 + 1, in a horizontal or slightly inclined line, #3 slightly elevated relative to first ACB. ACB 10–12. Minute scalloping of ventral margin of dentary. Other characters, in combination: Gill rakers 17–21. Posttemporal spine single, length moderate. Anal-fin pterygiophore spines long, needlelike. Photophore scale denticles absent. ACC photophores separated by gaps approaching the diameter of one photophore.

Description.—Body size moderate, largest examined 55.9 mm SL. D (14) 14–15. A (16) 16–18. P 13–14. V 6–7. GR 5–6 + 12–15 = (19) 17–21. Vertebrae (33) 33–34.

Ventral margins of all photophore scales smooth, without denticles. OVB 1 +

1 + 1, in an anteriorly-inclined straight line. ACA 1 + 1 + 1, separate (not united in a common organ), arranged in a horizontal to slightly inclined straight line. ACB (11; 10–12), with a slight dorsal step between #3 and #4. ACC (4), reflectors separated by gaps approaching width of one photophore.

Similar Species.—*Polyipnus omphus* most closely resembles *P. laternatus* with which it shares moderately long posttemporal spines, presence of anal-fin pterygiophore spines and high gill raker counts. Like other members of the *omphus* species group, *P. omphus* always has three isolated ACA photophores that appear as an anterior continuation of the ACB cluster. In *P. laternatus* the posterior two of these photophores are usually joined and markedly disjunct from the ACB elements. *Polyipnus omphus* is distinguished from other members of the *omphus* group by the much shorter posttemporal spine (5.9–10.7 as compared with 10.0–16.1% SL total range) and much higher gill raker counts (17–21 compared with 11–15 total range).

Distribution.—Originally known from the western Indian Ocean (including type locality) and the central Pacific (Baird, 1971). New material reported here suggests that *P. omphus* is an equatorial species of Indonesia and the western Pacific in addition to the western Indian Ocean (Fig. 35). There are no records from the central or eastern Indian Ocean and parts of the western Pacific; such range gaps could represent real disjunction or collection artifacts.

Remarks.—Although not specifically designated by Baird (1971: 94–96) in his description of *P. omphus* the 35.1 mm specimen taken with the holotype at DISCOVERY Sta. 5509 is assumed to be a paratype. It is labelled as such in the collection of the Museum of Comparative Zoology, Harvard University.

Baird (1971) stated that the specimen he examined from the central Pacific Ocean (SIO 60-236-10) was "slightly different phenotypically" from Indian Ocean material. Additional collections from Indonesia and the central Pacific examined here indicate that any morphometric or meristic distinctiveness of the SIO specimen is probably due more to a small sample size than any geographic trend or disjunction in morphological variation.

Polyipnus unispinus Schultz, 1938
Figure 41

Polyipnus unispinus Schultz, 1938: 137–138, 142 (fig. 43, holotype); 1961: 643–644 (fig. 20, holotype).—Baird, 1971: 97 (fig. 73, holotype).—Harold, 1990a: 1114; 1990b: 515.
Polyipnus sp.—Weitzman, 1974: 344 (USNM 203345).

Type Material.—Holotype: USNM 103353 (1, 20.5 mm). Paratypes: USNM 103029 (5, 16.0–19.0 mm).

Other Material.—AMS I.19287-003 (2, 27.1–28.8 mm). AMS I.19284-007 (1, 35.2 mm). AMS I.19292-007 (5, 25.4–30.4 mm). IOAN uncat. (1, 33.2 mm), 05°49′N 152°53′E to 05°45′N 152°43′E, 1,050–0 m, VITYAZ Cr. 25, Sta. 3655, 21 Aug 1957. IOAN uncat. (1, 31.0 mm), 05°34′S 130°48′E, 1,500–0 m, VITYAZ Cr. 57, Sta. 7261, 19 Mar 1975. IOAN uncat. (2, 28.4–29.8 mm), 29°52′S 168°48′E to 29°49′S 168°53′E, 500–0 m, DMITRY MENDELEEV Cr. 16, Sta. 1261, 04 Jan 1976. IOAN uncat. (9, 21.2–33.9 mm), 02°36′S 147°35′E, 800–0 m, VITYAZ Cr. 50, Sta. 6437, 14 May 1971. LACM 44481 (18, 16.0–32.0 mm). LACM 38588 (4, 20.0–30.0 mm). LACM 44503 (1, 33.0 mm). LACM 44469 (3, 32.0–35.0 mm). LACM 44481 (2, 33.0–35.0 mm). LACM 44486 (4, 16.0–29.0 mm). MCZ 64702 (1, 36.0 mm). MCZ 64703 (1, 28.9 mm). MCZ 64706 (5, 27.5–33.2 mm). MCZ 89816 (1, 24.4 mm). MCZ 89817 (2, 31.9–34.5 mm). MCZ 89818 (1, 25.6 mm). MCZ 89822 (1, 29.9 mm). SIO 61-31-108 (1, 31.6 mm). ZMUC P206964 (1, 21.4 mm). ZMUC P206965 (2, 21.5–34.3 mm). ZMUC P207119 (1, 30.4 mm).

Diagnosis.—Autapomorphies: Ventral margin of dorsomedian pigment essentially

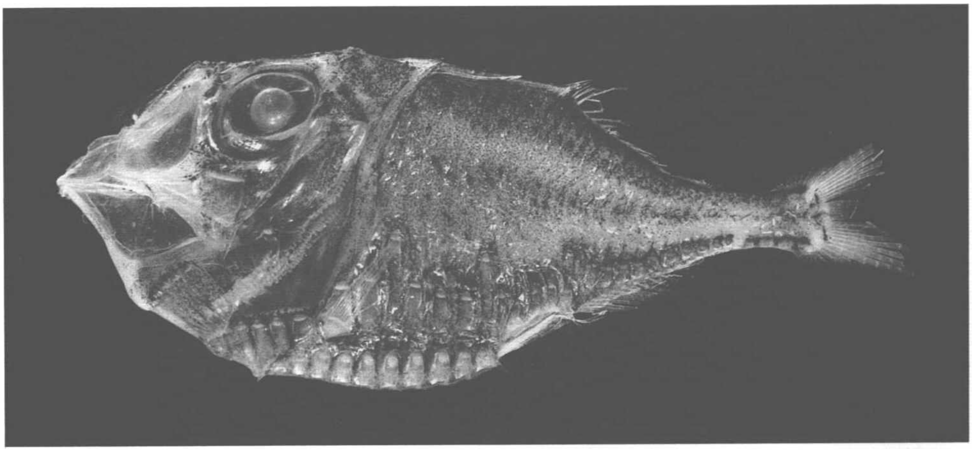

Figure 41. *Polyipnus unispinus*, AMS I.19287-003, 27.1 mm.

straight from pectoral girdle to caudal peduncle. Anal-fin pterygiophore spines long, needlelike. Minute denticles restricted to ventral surface of PV photophore scales. ACB photophores (9/10), posterior three to five appearing isolated and not interconnected. Lateral ridges of anterior and dorsal preopercular rami serrate. Other characters, in combination: Gill rakers 11/12. Posttemporal spine elongate. ACA 1 + 1 + 1, not connected to but appearing continuous with ACB cluster. ACC photophore reflectors separated by broad gaps.

Description.—Miniature species, maximum adult body size 35.2 mm SL. D (12) 11–13. A (14) 13–15. P (12) 12–13. V (7) 6–7. GR 4 + 7/8 = (12) 11–12. Vertebrae 35/36.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. OVB 1 + 1 + 1, in an anteriorly-inclined straight line. PV scale ventral margins with minute denticles. ACA 1 + 1 + 1, separate (not united as a cluster), in anteriorly-inclined straight line or with #1 and #2 adjacent and elevated relative to #3; not connected to first ACB. ACB (9; 9–10), the posterior three to five photophores appearing isolated and not interconnected by lumena. ACC (4), reflectors separated by spaces greater than diameter of one photophore.

Similar Species.—*Polyipnus unispinus* is most similar to *P. danae* and *P. aquavitus.* These three miniature species do not exceed 40 mm, have single, long, slender posttemporal spines and reduced numbers of gill rakers (11–15). The former two species are closest, both having highly elongate, rodlike caudal peduncles and 11 or 12 gill rakers. *Polyipnus unispinus* is distinguished from *P. danae* by the presence of anal-fin pterygiophore spines and PV photophore scale denticles. It is distinguished from all congenerics by the lack of a lateral pigment bar. *Polyipnus unispinus* is the only species outside of the *P. spinosus* species group with photophore scale denticles. These last two characters can be used effectively for identification of specimens as small as 10 mm SL.

Distribution.—*Polyipnus unispinus* occurs in the Java Trench, Timor, Halmahera, Sulu and Celebes Seas, the New Britain Trench (off the Solomon Islands), southeastward to New Caledonia and with a few captures to the north of New Zealand (Fig. 39). This species has not been collected in the South China Sea (adjacent to the Sulu Sea). Collections from Indonesia made with discrete-depth sampling

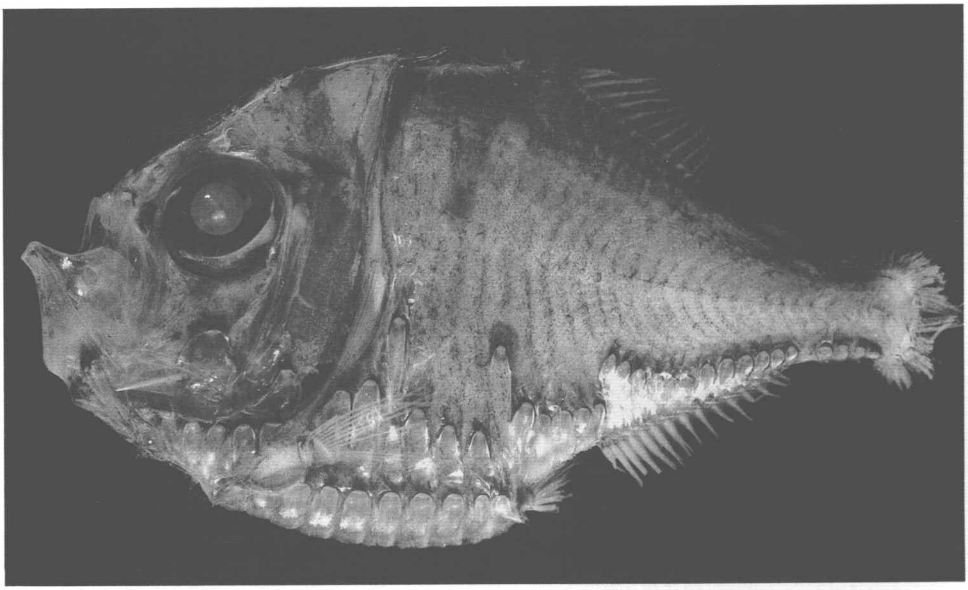

Figure 42. *Polyipnus asper*, holotype, USNM 273282, 62.1 mm.

gear indicate a bathymetric range of 300–500 m by day, however, one night sample from the Sulu Sea (ALPHA HELIX Sta. 177, 1975) shows *P. unispinus* within 50 m of the surface. This suggests that either significant vertical migration takes place or that the species has a shallow depth distribution in the Sulu Sea (Harold, in prep.). Anomolous shallow depth distributions for many deep-sea taxa, including sternoptychids, in the nearby Banda Sea have been reported by van der Spoel and Schalk (1988).

Remarks.—The presence of minute denticles on the ventral surfaces of the PV photophore scales which also occurs throughout the *spinosus* species group is not regarded here as an indication of close relationship. The position of *P. unispinus* within the *P. omphus* species group is well corroborated. It therefore seems likely that denticles on the PV photophore scales have arisen in this species independently of such structures in the other group.

Polyipnus spinosus species group

Fourteen species endemic to various oceanic areas from the western Indian Ocean through the Indo-Pacific region and east to the Hawaiian Islands and the East Pacific Rise: *P. asper, P. elongatus, P. fraseri, P. indicus, P. inermis, P. nuttingi, P. oluolus, P. parini, P. paxtoni, P. soelae, P. spinifer, P. spinosus, P. stereope, P. tridentifer.*

Polyipnus asper new species
Figure 42

Type Material.—Holotype: USNM 273282 (1, 62.1 mm), 10°39′N 46°35′E, 0–384 m, ANTON BRUUN, Cr. 1 (International Indian Ocean Expedition), Sta. 23, 24 Mar 1963. Paratypes: USNM 304746 (30, 28.0–54.9 mm), same data as holotype. IOAN uncat. (15, 26.5–58.0 mm), 10°42.4′N 96°43.7′E, AKADEMIK KNIPOVICH Sta. 452, 11 Mar 1966.

Diagnosis.—Autapomorphies: Minute spine on ventral margin of anguloarticular immediately anterior to retroarticular. Mesopterygoid smooth, pitting reduced. First infrapharngobranchial subcylindrical. Other characters, in combination: Gill rakers 17–20. Lateral pigment bar tapered and long, approaching but not reaching lateral midline. Two posttemporal spines: dorsal spine long, basal spine length less than half of that of dorsal spine. Anal-fin pterygiophore spines absent. Photophore scale denticles restricted to PV, VAV, ACB and ACC clusters. ACB 8–10. ACC compact. Two-spined longitudinal parietal keel present.

Description.—Moderate-sized species, maximum adult body size 62.1 mm SL. D (13) 12–13. A (16) 15–17. P (13) 12–13. V (7) 6–7. GR (6 + 13) 5–6 + 12–14 = (19) 17–20. Vertebrae (33) 33. Body profile anterior of dorsal fin and pelvic fin subrectangular, slightly tapered anteriorly, acutely tapered posteriorly as far as caudal peduncle. Profile of caudal peduncle rectangular, elongate in anterior-posterior axis. Ventral margin of dentary with two serrate keels. Margins of dentary and premaxillary with minute, recurved teeth. Maxillary teeth shorter, conical. Palatine teeth absent. Anterior region of vomer with 16–20 longitudinal rows of minute conical teeth in a transverse patch. No teeth present on posteromedian process of vomer. Parietal keel discontinuous; anterior region keel-like, posterior region with two conical spines in the median plane, directed anteriorly and posteriorly. Posttemporal limbs with two parallel serrate ridges and supporting two spines: dorsal spine serrate, long (5.7–12.2% SL), and curved dorsally, ventral spine short (usually less than half of the length of the dorsal spine), nonserrate, ventrolaterally directed. Ventral margin of pectoral shield with 5–11 conical spines. Vertical and anteroventral rami of preopercle each with two parallel deeply serrate lateral ridges. Preopercle with two spines: ventral spine long (2.4–6.6% SL), anteriorly curved, directed anteroventrally; dorsal spine short (not longer than one preopercular serration), directed laterally. Dorsal spinous process smooth or with a single spine-like serration, exposed length and height about equal, terminating posterodorsally as two conical dorsolaterally-directed spines (one per side). Anal-fin pterygiophore spines absent.

Morphometric characters (% SL): Head length 31.2–39.4, orbit length 13.7–18.4, body depth 58.8–68.0, caudal-peduncle depth 9.6–12.9, caudal-peduncle length 13.2–20.0, dorsal-fin length 19.2–25.7, anal-fin length 21.9–25.6, preanal length 67.8–76.0, predorsal length 56.2–62.1, preventral length 63.2–74.8, postdorsal length 49.5–61.9, postanal length 37.9–42.9, ACC length 6.7–9.1, ACB-C length 1.9–3.5.

Ventral margins of photophore scales smooth, except PV, VAV, and ACC which have numerous denticles, and ACB which have one to three denticles per scale. OVB 1 + 1 + 1, in an anteriorly-inclined straight line. ACA 1 + 1 + 1, #1 and #2 isolated, but aligned with #3 and first three ACB. ACA #3 united with ACB forming a continuous organ: ACA photophores appear to grade into ACB. ACB (9; 8–10), with dorsal step between #3 and #4.

Dark pigment saddle with predorsal notch and moderately long lateral pigment bar tapering toward but not reaching lateral midline.

Similar Species.—Four species of the *P. spinosus* species group have posttemporals with two spines: *P. asper, P. indicus, P. nuttingi,* and *P. oluolus. Polyipnus asper* most closely resembles *P. indicus* in overall body form, photophore patterns and fin-ray counts. The present species is distinguished from *P. indicus* by the presence of denticles on scales of the ACB photophore cluster and two opposed median spines representing the modified posterior region of the parietal keel. Two other species, *P. parini* and *P. inermis,* have body shapes and photophore com-

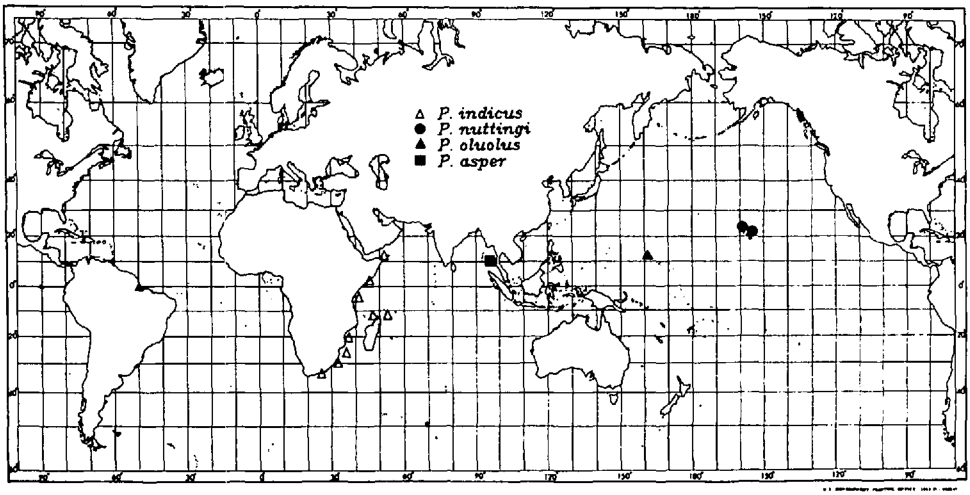

Figure 43. Collection station localities for *P. indicus, P. nuttingi, P. oluolus* and *P. asper, P. spinosus* species group.

plements that are similar to those of *P. asper* but they have three posttemporal spines and a broad gap separating the third and fourth ACB photophores.

Distribution.—*Polyipnus asper* is known from one ANTON BRUUN and one AKADEMIK KNIPOVICH station off the west coast of the Malay Peninsula in the Andaman Sea (Fig. 43). These collections were made 3 years apart at approximately the same position. The maximum depth of capture for the type series is 384 m.

Remarks.—*Polyipnus asper* is probably more widely distributed in the eastern Indian Ocean but has gone undetected because of low sampling density in the region. Most expeditions (e.g., DANA, 1928–1930) made very few collections and only along a single west-east line which passed to the south of Sumatra. In that area several other *Polyipnus* taxa have been collected albeit not members of the *P. spinosus* species group (i.e., *P. meteori, P.* aff. *triphanos, P. unispinus*). Numerous collections made off the northwest coast of Australia have yielded *P.* aff. *kiwiensis* and large numbers of a new species, *P. soelae.*

Günther (1887) listed a reference to *P. spinosus* from the Bay of Bengal and although such a western occurrence of that species cannot be ruled out the species referred to is more likely to have been *P. asper.*

Etymology.—The epithet *asper* is a Latin adjective meaning rough, referring to the presence of denticles in the ACB photophore scales.

Polyipnus elongatus Borodulina, 1979
Figure 44

Polyipnus elongatus Borodulina, 1979: 8–9 (holotype fig. 5).—Harold, 1989: 874–875; 1990b: 515.—Paxton et al., 1989: 192.

Type Material.—Holotype: ZIL 43999 (1, 59.0 mm) (x-radiograph examined only). Paratypes: ZIL 44001 (1, 51.0 mm) (x-radiograph examined only).

Other Material.—AMS I.21795-007 (5, 54.6–68.8 mm). AMS I.20518-005 (2) (not seen, apparently lost).

Diagnosis.—Autapomorphies: Large dorsal posttemporal spine with large tooth-

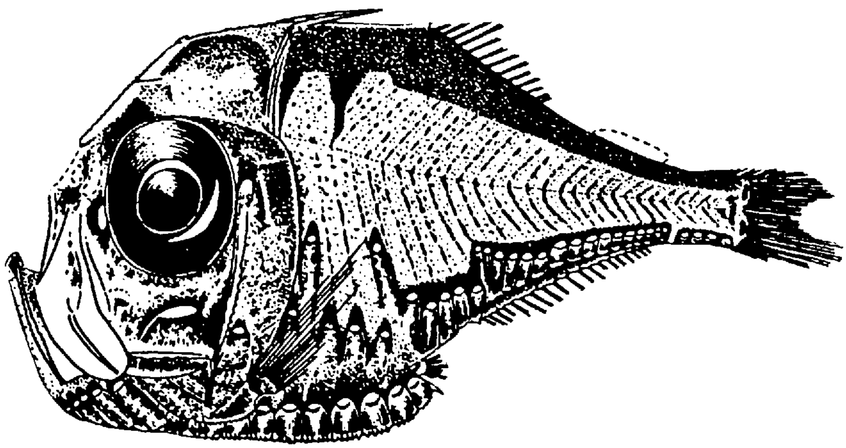

Figure 44. *Polyipnus elongatus*, holotype. Reproduced with permission, from Borodulina (1979).

like serrations. Diagonal ridge of preopercle with several prominent serrations. Body profile highly tapered posteriorly. Other characters, in combination: Gill rakers 22–24. Lateral pigment bar tapered and long, approaching but not reaching lateral midline. Three posttemporal spines: dorsal long, median and ventral spines subequal, about ¼ length of dorsal spine. Photophore scale denticles restricted to PV and VAV clusters. ACA photophores grade into ACB. ACB 13 or 14. ACC photophores separated by conspicuous gaps.

Description.—Adult body size moderate to large, maximum about 70 mm SL. D (13) 13–14. A (19) 17–20. P (13) 12–13. V 7. GR 7 + 15/16 = (23) 22–24 (24 from Borodulina, 1979). Vertebrae (35) 35.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. OVB 1 + 1 + 1, in an anteriorly-inclined straight line. PV scale ventral margins with spinelike denticles. L 1. VAV (5), ventral margins of scales denticulate. ACA 1 + (2), in an anteriorly-inclined straight line: #1 isolated, not connected to #2 by a lumen; #2 and #3 connected to each other and to ACB, appearing as a continuous cluster of photophores. ACB (14; 13–14), with an indistinct dorsal step between #3 and #4. ACC without denticulate scales, conspicuous gaps separating each photophore reflector.

Similar Species.—*P. elongatus* bears some similarity to *P. spinosus* sensu stricto with regard to pigmentation and, superficially, the spines of the posttemporal bone. *P. elongatus* is most similar to *P. paxtoni*, particularly with respect to photophore patterns, pigmentation and posttemporal spine configuration. These two species are the only members of the genus with two highly reduced, subequal median and ventral posttemporal spines. *P. elongatus* differs in its higher ACB photophore counts and lack of denticles throughout the AC cluster.

Distribution.—*P. elongatus* has been collected only in the western Coral Sea, off the east coast of Queensland, Australia (Fig. 45). Available records suggest that this species occurs above 440 m.

The range of *P. elongatus* probably overlaps with *P. paxtoni* and *P. triphanos* and possibly *P. unispinus* and *P. aquavitus*.

Remarks.—According to Borodulina (1979: 9), *P. elongatus* is most similar to *P.*

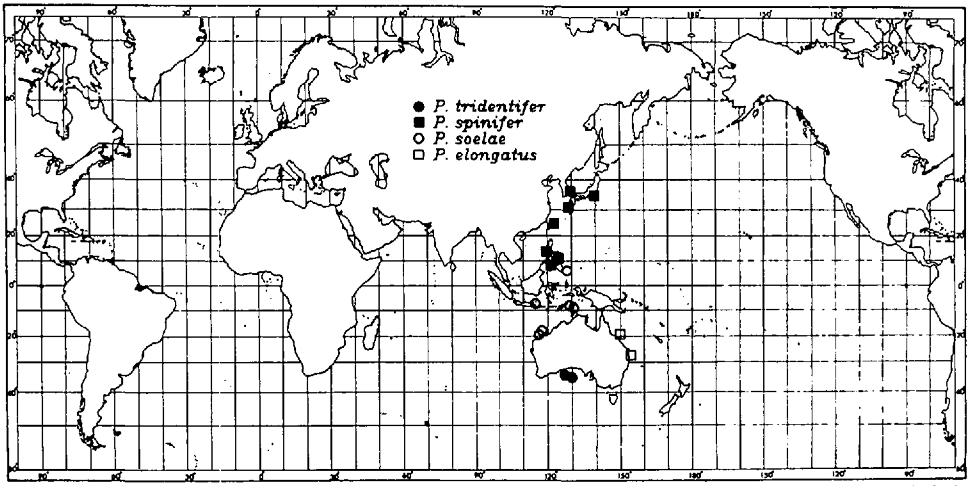

Figure 45. Collection station localities for *P. tridentifer, P. spinifer, P. soelae* and *P. elongatus, P. spinosus* species group.

spinosus. However, the material that she listed and described for the latter species had denticulate ACC photophore scales, a feature which is not evident in the holotype of *P. spinosus,* other material reported here or by Bourret (1985). The specimens mistaken for *P. spinosus* by Borodulina have been examined and are attributed to a new species, *P. soelae.*

Polyipnus fraseri Fowler, 1934
Figure 47

Polyipnus fraseri Fowler, 1934: 257–258.—Parr, 1937: 55.—Schultz, 1938: 142, 145; 1961: 642; 1964: 267.—Yamamoto, 1982: 327.—Fujii, 1984: 47 (pl. 49L).—Harold, 1989: 874–875; 1990b: 509–515 (holotype fig. 2).

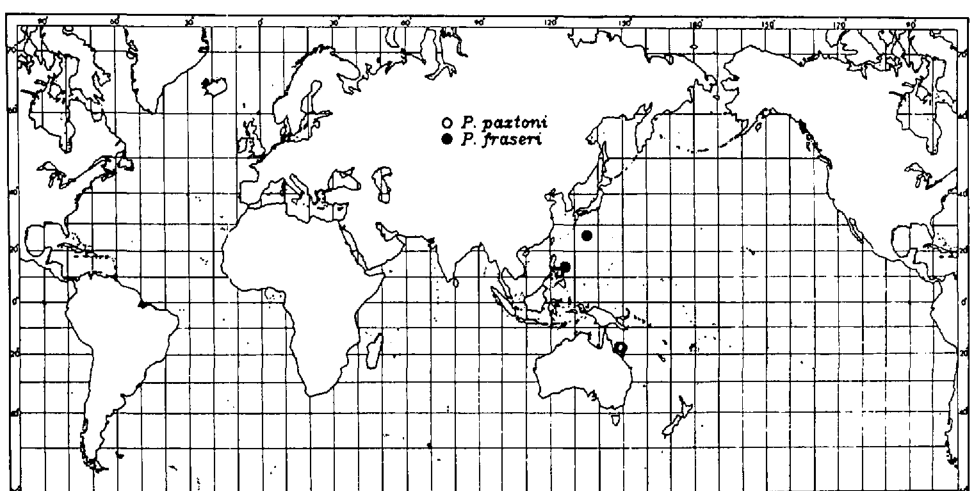

Figure 46. Collection station localities for *P. paxtoni* and *P. fraseri, P. spinosus* species group.

Polyipnus tridentifer.—Baird, 1971: 86 (part, incorrect subsequent spelling and year in synonymy: *Polyipnus frazeri* Fowler, 1933).
Polyipnus spinosis.—Borodulina 1979: 7–8 (part, incorrect subsequent spelling of *Polyipnus spinosus*).

Type Material.—Holotype: USNM 92324 (1, 40.4 mm SL).

Other Material.—BSKU 29353 (1, 32.4 mm SL).

Diagnosis.—Autapomorphies: Dorsal-fin rays 10. Two dark lateral pigment bars on flank, anterior projection broad with a rounded termination ventral of lateral midline, posterior projection short and tapered. Unique posterior preopercular spine. Eye relatively large, orbit length about one quarter of standard length. ACA photophores absent. ACB (4). ACC compact. Other characters, in combination: Gill rakers 19/20. Three posttemporal spines. PV, VAV, ACB and ACC photophore scales with numerous denticles.

Description.—Adult body size small to moderate, largest specimen 40.4 mm. D (10) 10. A (11) 12. P (14) 14. V (7) 6. GR 6/7 + 13 = (20) 19.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. OVB 1 + 1 + 1, stepped dorsally in approximately equal increments from anterior to posterior. PV, VAV, ACB and ACC photophore scales with numerous denticles over lateral and ventral surfaces. ACA photophores absent. ACB (4; 4). ACC (4), compact.

Similar Species.—*P. fraseri* is a member of the *P. spinosus* species group, characterized in part by the presence of a multispinose (two or three spines) posttemporal. Arrangement and shape of posttemporal spines in *P. fraseri* is most similar to that of *P. spinifer, P. soelae, P. spinosus* and *P. stereope,* all of which have large dorsal and prominent, but much shorter, basal spines. *P. fraseri* is distinguished from these and all other species by the presence of a unique posterior preopercular spine, absence of ACA photophores, and only four ACB photophores at standard length over 20 mm.

Distribution.—This species has been collected at two stations; off the east coast of the Philippines and in the central Philippine Sea near the Kyushu-Palau Ridge (Fig. 46). Maximum depth of capture of the holotype is about 1,000 m but the second specimen was taken above 340 m which is closer to the bathymetric ranges of other species.

The geographic ranges of *P. triphanos, P. unispinus, P. spinifer* and *P. matsubarai* may overlap with that of *P. fraseri.*

Remarks.—Capture of a second specimen has contributed to the recognition of *P. fraseri* as a distinct species (Harold, 1990b). The present redescription reiterates morphological and ontogenetic evidence which also lead to this conclusion. Usually only a juvenile (up to about 15 mm SL) would have as few as 4 ACB photophores. Appearance of new photophores usually occurs at body sizes up to 30 mm SL (lowest ACB count in other species at that standard length is 7). Rate of photophore budding is probably quite low in *P. oluolus* as well (6 ACB photophores at 26.9 mm SL, only known specimen). The largest individual of another species with no ACA photophores is 16.9 mm SL (*P. ruggeri*). With so much interspecific and ontogenetic variation in photophore number, and only one specimen known, Baird (1971) and Borodulina (1979) believed they were taking a conservative approach in synonymizing *P. fraseri* with *P. tridentifer* and *P. spinosus,* respectively.

Relative size of various elements of the skull are also atypical and seem to be correlated with enlargement of the eye. As percentages of standard length, *P.*

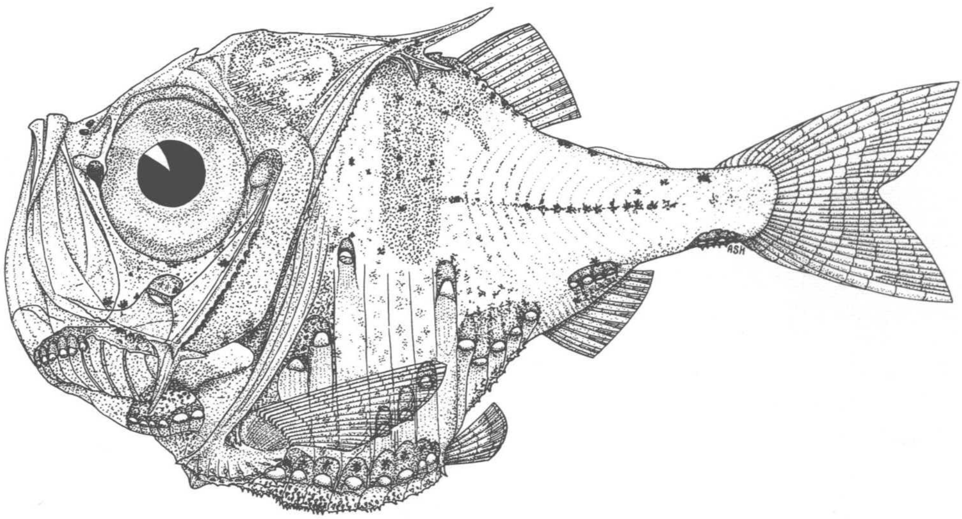

Figure 47. *Polyipnus fraseri,* USNM 92324, 40.4 mm. Reproduced from Harold (1990b).

fraseri has an orbital length of 18.0 to 23.0, 13.6 to 19.0 in other species at SL less than 25 mm, and 10.8 to 17.2 in other species at SL greater than 25 mm.

Polyipnus indicus Schultz, 1961
Figure 48

Polyipnus nuttingi.—Norman, 1939: 20 (part).
Polyipnus indicus Schultz, 1961: 645–646 (holotype fig. 22); 1964: 268.—Baird, 1971: 91–92 (fig. 68); 1986: 25 (fig. 75.8).—Harold, 1989: 874–875; 1990b: 515.
? (non) *Polyipnus spinosus.*—Reimer, 1985: 225 (parasites).

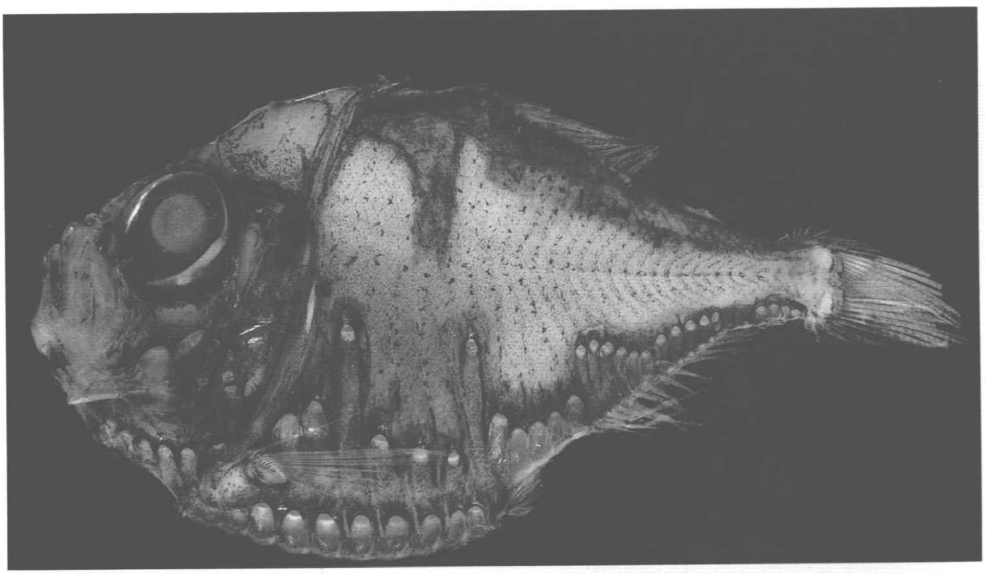

Figure 48. *Polyipnus indicus,* ROM uncat., 62.3 mm.

Type Material.—Holotype: BMNH 1939.5.24.403 (1, 37.0 mm). Paratypes: BMNH 1939.5.24.404 (1, 38.2 mm) and USNM 179897 (1, 46.2 mm).

Other Material.—ARC 8909384 (4, 52.0–63.0 mm). CAS 66558 (4, 46.0–57.0 mm). IOAN uncat. (15, 34.3–48.7 mm), 25°30.4′S 35°08′E to 25°34.2′S 35°01.5′E, (0–) 570–500 m, VITYAZ Cr. 17, Sta. 2631, 1342–1500 h, 23 Nov 1988. IOAN uncat. (25, 33.7–42.0 mm), 12°17.5′N 53°14.5′E to 12°17.5′N 53°06.5′E, (0–) 364–384 m, VITYAZ Cr. 17, Sta. 2566, 1330–1426 h, 28 Oct 1988. MNHN 1988-1322, -1326, -1327 and -1328 (1, 48.6 mm; 1, 42.6 mm; 1, 49.8 mm; 1, 41.2 mm), 12°28′S 48°12′E, (0–) 605 m, LE VAUBAN Sta. 21, 1972. ROM uncat. (5, 53.6–62.3 mm), 21°12.8′S 35°41.8′E to 21°16.6′S 35°41.3′E, 480–500 m, VITYAZ Sta. 2622, 0215–0418 h, 26 Dec 1988. USNM 293986 (3, 42.6–45.1 mm). USNM 301277 (5, 23.3–30.7 mm). ZMUC P206973 (1, 13.0 mm). ZMUC P206922 (10, 31.0–47.0 mm). ZMUC P206924 (5, 38.0–49.0 mm).

Diagnosis.—Autapomorphies: Shallow but abrupt incision in midventral surface of maxilla for attachment of posterior process of premaxilla. Supraoccipital posteromedian process absent. Dorsal spinous process finely serrate. Posteriormost anal-fin proximal radial short. Other characters, in combination: Gill rakers 19–21. Lateral pigment bar tapered and long, usually reaching lateral midline. Two posttemporal spines: dorsal spine long, basal spine length less than half of that of dorsal spine. Photophore scale denticles restricted to PV, VAV and ACC clusters. ACB 7–9. ACC compact. Parietal keel spines absent.

Description.—Adult body size moderate, reaching more than 60 mm SL. D (14) 12–14. A (16) 15–16. P (13) 12–14. V 7. GR (7 + 13) 5–7 + 13–16 = (20) 19–21. Vertebrae 32–33.

Ventral margins of photophore scales smooth, except PV, VAV and ACC which have numerous denticles. OVB 1 + 1 + 1, in an anteriorly-inclined straight line. ACA 1 + 1 + 1, #1 and #2 isolated, but aligned with #3 and first three ACB. ACA #3 united with ACB #1 forming a continuous organ. ACB (8; 7–9), with a dorsal step between #3 and #4. ACC compact.

Similar Species.—*P. indicus* is most similar to *P. nuttingi, P. oluolus* and, especially, *P. asper.* These four are the only species in *Polyipnus* with two posttemporal spines. Of these, only *P. indicus* and *P. asper* have denticulate ACC photophore scales. *P. indicus,* unlike *P. asper,* has a simple, blade-like parietal keel (not differentiated posteriorly into two spines) and lacks ACB photophore scale denticles. In addition, *Polyipnus indicus* frequently has more gill rakers than *P. asper* (19–21 compared with 17–20).

Distribution.—Restricted to the western Indian Ocean off the east coast of Africa from Natal in the south and as far north as the Gulf of Aden (Fig. 43). To the east, *P. indicus* has been taken frequently off the north coast of Madagascar. Catch data indicate a bathymetric range of about 480 to 660 m but due to the use of open-tow gear these ranges should be viewed as maximum values.

Remarks.—*Polyipnus indicus* is the only representative of the *P. spinosus* species group occurring in the western Indian Ocean. Any references to *P. spinosus* (e.g., Reimer, 1985) or other presently recognized members of the group from this region are probably *P. indicus.* Baird (1971: 90) refers to questionable records of *P. spinosus* from off peninsular India but concluded that they were likely *P. tridentifer* (*P. soelae* of this account). The records in question could represent *P. indicus, P. asper* or an undescribed species. Specimens examined from the Gulf of Aden, here referred to *P.* cf. *indicus* (USNM 293986 and 301277), exhibit some variation in parietal ornamentation which may, on further study, reveal the presence of an undescribed species.

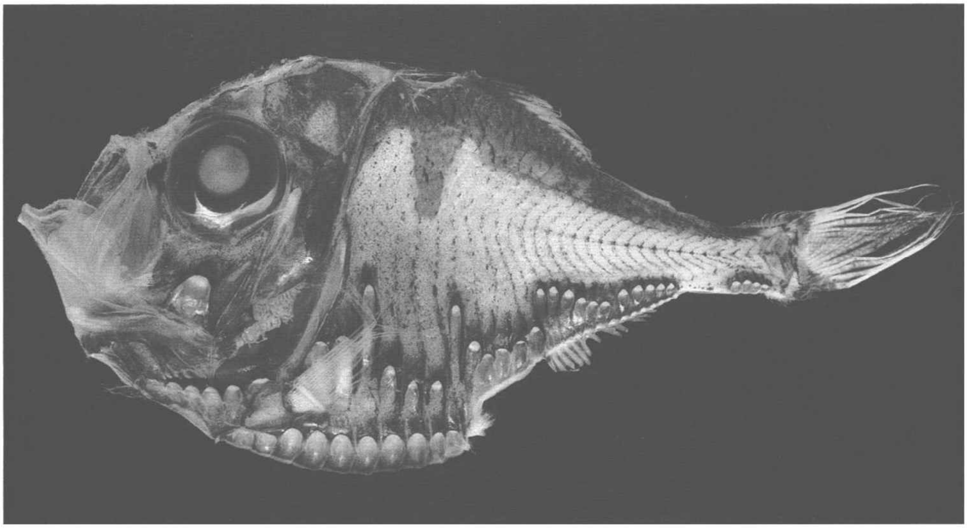

Figure 49. *Polyipnus inermis*, IOAN uncat., PROFESSOR SHTOKMAN Cr. 18, Sta. 1965, 51.5 mm.

Polyipnus inermis Borodulina, 1981
Figure 49

Polyipnus inermis Borodulina, 1981: 122–124 (holotype fig. 1).—Harold, 1989: 874–875; 1990b: 515.

Type Material.—Holotype: MMSU P-15413 (1, 39.0 mm), (x-radiograph only). Paratypes: IOAN uncat. (5, 40.0–63.5 mm), 25°01'S 88°27'W, 535–575 m, IKHTIANDR trawl no. 54 (not seen).

Other Material.—ROM uncat. (3, 48.9–49.4 mm), 24°58'S 88°29'W, (0–) 562–545 m, PROFESSOR SHTOKMAN Sta. 1965, 30 Apr 1987. IOAN uncat. (15, 38.3–50.6 mm), same data as previous entry. IOAN uncat. (3, 49.2–56.2 mm), 25°25'S 86°32'W, 420–0 m, IKHTIANDR Cr. 5, trawl 57, 31 Oct 1979. IOAN uncat. (2, 37.9–43.0 mm), 25°03.4'S 88°38.1'E, 545–0 m, GERAKL, 1350 h, 04 Nov 1975.

Diagnosis.—Autapomorphies: Anterodorsal surface of dorsal spinous process smooth, without seration. Ventral margin of anguloarticular finely serrate. ACB photophore scale denticles absent. Lateral ridge of dentary entire, unornamented. Other characters, in combination: Gill rakers 23–26. Lateral pigment bar tapered and long, terminating bluntly at or near lateral midline. Posttemporal spines 3, subequal, tridentlike: dorsal spine (8.0–9.0% SL). Photophore scale denticles restricted to PV cluster. ACB 8–10, with a gap about equal to the width of one photophore between #3 and #4. ACC photophores compact.

Description.—Maximum adult body size 63.5 mm SL. D (12) 12–13. A (16) 16/17. P (14) 14–15. V 7. GR 6–8 + 16–17 = (24) 23–26 (25 and 26 values reported by Borodulina, 1981). Vertebrae (34).

Ventral margins of photophore scales smooth, except PV cluster which is sparsely and weakly denticulate. Photophore counts: OVB 1 + 1 + 1, in an anteriorly-inclined straight line. ACA 1 + 1 + 1, #1 and #2 isolated, but aligned with #3 and first three ACB. ACA #3 united with ACB #1, forming a continuous organ. ACB (8; 8–10), with a dorsal step and a broad gap about equal to the width of one photophore between #3 and #4.

Similar Species.—*P. inermis* is one of several species in the genus that have three subequal posttemporal spines. The others are *P. parini* and *P. tridentifer*. In some

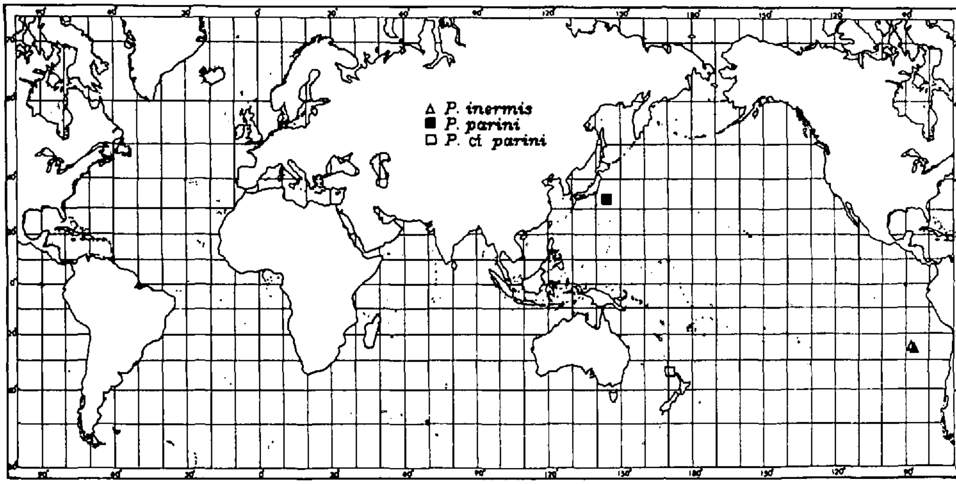

Figure 50. Collection station localities for *P. inermis, P. parini* and *P.* cf. *parini, P. spinosus* species group.

instances the spine configuration of *P. spinifer, P. soelae* and *P. stereope* may approach this condition but the median spine is always noticeably shorter than the dorsal. In contrast to these posttemporal characters, the presence of a dorsal step between the third and fourth ACB photophores is similar to *P. oluolus, P. nuttingi, P. indicus* and *P. asper* (of the *spinosus* species group). *Polyipnus inermis* and *P. parini* are most similar, sharing a unique gap (about equal to the width of one photophore) between photophores #3 and #4 of the ACB cluster. *Polyipnus inermis* is distinguished from *P. parini* by a lack of denticles on the scales of the VAV photophores and lower gill raker counts (23–26 compared with 28 or 30, respectively).

Distribution.—*Polyipnus inermis* has been collected at several stations only in the vicinity of the Sala-y-Gomez Submarine Ridge, eastern South Pacific Ocean (Fig. 50). Available data indicate that *P. inermis* occurs above 420 m, and possibly as deep as 575 m.

Remarks.—Borodulina (1981: 124) stated that *P. inermis* is "closest" to *P. parini* but provided no direct comparisons with other species. As indicated in her earlier paper (Borodulina, 1979) on the "*spinosus* complex," there is a broad space between the anal (=ACB) and subcaudal (=ACC) photophores in *P. parini* (also present in *P. inermis*) distinguishing it from other members of the complex (except *P. fraseri,* which was not recognized by Borodulina, 1979). More distinctively, *P. inermis* and *P. parini* possess a unique gap in the ACB photophore cluster, between the third and fourth photophores (a synapomorphy). Apparent reduction of PV photophore scale denticles in *P. inermis* is unusual for members of the *spinosus* group. Another peculiarity is the extensive horizontal predorsal surface of the body: this part of the dorsal profile is convex in other species.

Polyipnus nuttingi Gilbert, 1904
Figure 51

Polyipnus nuttingi Gilbert in Jordan and Starks, 1904: 581 (AC photophores, posttemporal process and pigmentation compared with that of *P. stereope*)

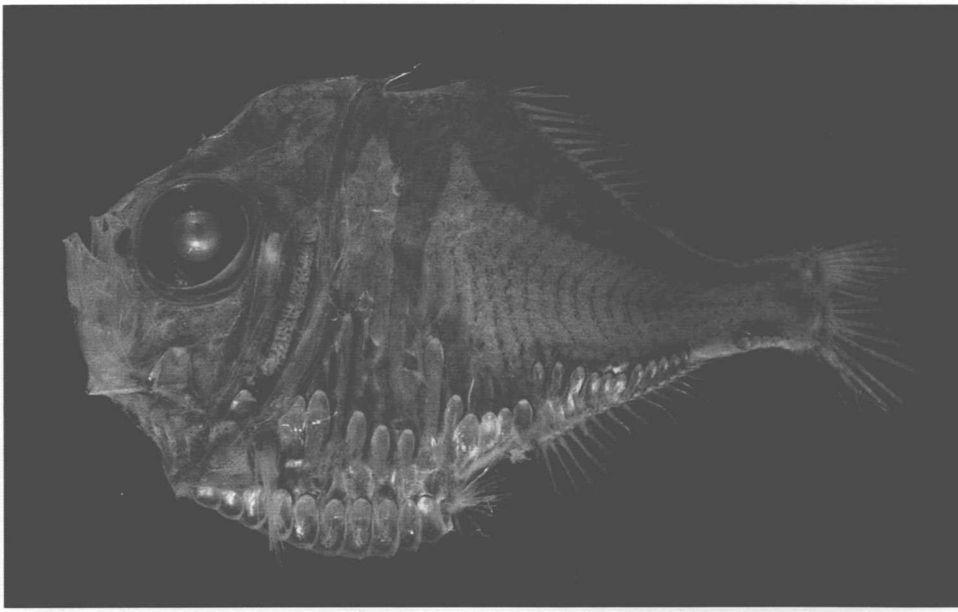

Figure 51. *Polyipnus nuttingi*, BPBM 24892, 37.9 mm.

Polyipnus nuttingi.—Gilbert, 1905: 609–610 (holotype pl. 73).—Schultz, 1938: 142, 145.—Norman, 1939: 20.—Schultz, 1961: 645 (fig. 21); 1964: 268.—Baird, 1971: 92 (fig. 69).—Harold, 1989: 874–875; 1990b: 515.

Type Material.—Holotype: USNM 51599 (1, 83.0 mm). Paratypes: USNM 51693 (29, 33.5–69.5 mm). AMNH 3548 (1, 55.5 mm).

Other Material.—BPBM 24892 (3, 28.3–39.9 mm). BPBM 23779 (2, 47.1–48.5 mm). BPBM 23790 (7, 47.6–60.5 mm). BPBM 24005 (7, 38.1–55.5 mm).

Diagnosis.—Autapomorphies: Lateral surface of parhypural with minute spines. Dorsal posttemporal spine lateral margins with deeply sculpted serrations. Other characters, in combination: Gill rakers 20–24. Lateral pigment bar tapered and long, usually reaching ventrally of lateral midline. Two posttemporal spines: dorsal spine moderately long, deeply serrate margins; basal spine highly reduced, inconspicuous. Photophore scale denticles restricted to PV and VAV clusters. ACB 7–9. ACC photophores compact. Frontal-parietal keel continuous and evenly serrate.

Description.—Maximum adult body size moderate to large, up to 83.0 mm SL (holotype). D (13) 12–13. A (17) 16–17. P (13) 12–14. V 7. GR 6–8 + 14–16 = (22) 20–24. Vertebrae 33/34.

Ventral margins of photophore scales smooth except PV and VAV: PV finely denticulate, VAV smooth or with blunt denticles. OVB 1 + 1 + 1, in an anteriorly-inclined straight line. ACA 1 + 1 + 1, #1 and #2 isolated, but aligned with #3 and first three ACB. ACA #3 united with ACB cluster, forming a continuous organ. ACB (8; 7–9), with a pronounced dorsal step between #3 and #4. ACC compact.

Similar Species.—*P. nuttingi* is similar to *P. indicus*, *P. asper*, and *P. oluolus* which all have a large serrate dorsal posttemporal spine with a single minute basal secondary spine. This contrasts with Baird's (1971: 92) description in which the

secondary spine in *P. nuttingi* was not distinguished from adjacent serrations. *P. nuttingi* and *P. oluolus* are the only two species of the above that lack denticles on the ACC photophore scales. *P. nuttingi* is distinguihed from *P. oluolus* by the long pigment bar (*P. oluolous* appears to lack a lateral pigment bar), higher numbers of ACB photophores (7–9 as compared with 6), and a much shorter dorsal posttemporal spine (5.5–7.0 as compared with 17.0% SL).

Distribution.—*P. nuttingi* is restricted to the slope and channel areas of the Hawaiian Islands (Fig. 43) at depths of about 400 to 570 m. Although this is the only representative of the genus known to occur in the Hawaiian Islands several species (*P. omphus, P. meteori,* and *P. matsubarai*) that have broad ranges may also occur in the area. In particular, *P. matsubarai* has been collected near the Hawaiian-Emperor Seamounts (NMFSH P-1002): if this spcies has populations in the Hawaiian Islands they are probably ecologically and/or geographically disjunct from *P. nuttingi,* given the relatively large number of collecting stations at which only the latter was present.

Remarks.—According to Schultz (1961) the collection of "cotypes" listed below as paratypes (USNM 51693) is an amalgamation of specimens taken at a number of ALBATROSS stations and consequently no precise locality can be given. Each specimen has a numbered tag but their significance is not known. Gilbert (1905: 610) lists localities descriptively and trawling depths for the contributing collections. One additional ALBATROSS collection (AMNH) which was received by the American Museum of Natural History in 1907 appears to come from the original set of collections and may be a paratype. The specimen was sent to AMNH on exchange from the Smithsonian Institution (USNM) but neither the details of the transaction nor the exact source of the specimen are known.

Polyipnus oluolus Baird, 1971
Figure 52

Polyipnus oluolus Baird, 1971: 90–91 (holotype, fig. 67).—Harold, 1989: 874–875; 1990b: 515.

Type Material.—Holotype: USNM 204390 (1, 26.9 mm).

Diagnosis.—Autapomorphies: Lateral pigment bar absent, diffuse dark pigment dorsally. PV photophore scales with extensive triangular ventral margins with one or two denticles at apices. ACA photophores all separate and increase in elevation incrementally from anterior to posterior. ACB 6, posterior three isolated from each other, no interconnecting lumen. Other characters, in combination: Gill rakers 19. Two posttemporal spines: dorsal spine long, lateral margins deeply serrate, basal spine highly reduced, inconspicuous. ACC compact.

Description of Holotype.—Known only from holotype, 33.0 mm SL. D (14). A (14). P (13). V (6). GR (19).

Ventral margins of photophore scales smooth, except as noted below. OVB 1 + 1 + 1, #2 and #3 adjacent and at an elevation ventral to #1. PV scale ventral margins triangular and with one or two denticles at apices. VAV scales with extensive blade-like ventral margins. ACA 1 + 1 + 1, isolated, not united in a common organ, increasing in elevation from anterior to posterior, #3 located proximal to first ACB. ACB (3) + 1 + 1 + 1, with a dorsal step between #3 and #4, #1–#3 united. ACC compact, with extensive bladelike ventral margins.

Similar Species.—*P. oluolus, P. indicus, P. asper* and *P. nuttingi* are the only members of the genus with two posttemporal spines. The basal spine in *P. indicus* and *P. asper* is conspicuous whereas in *P. oluolus* and *P. nuttingi* it is very small

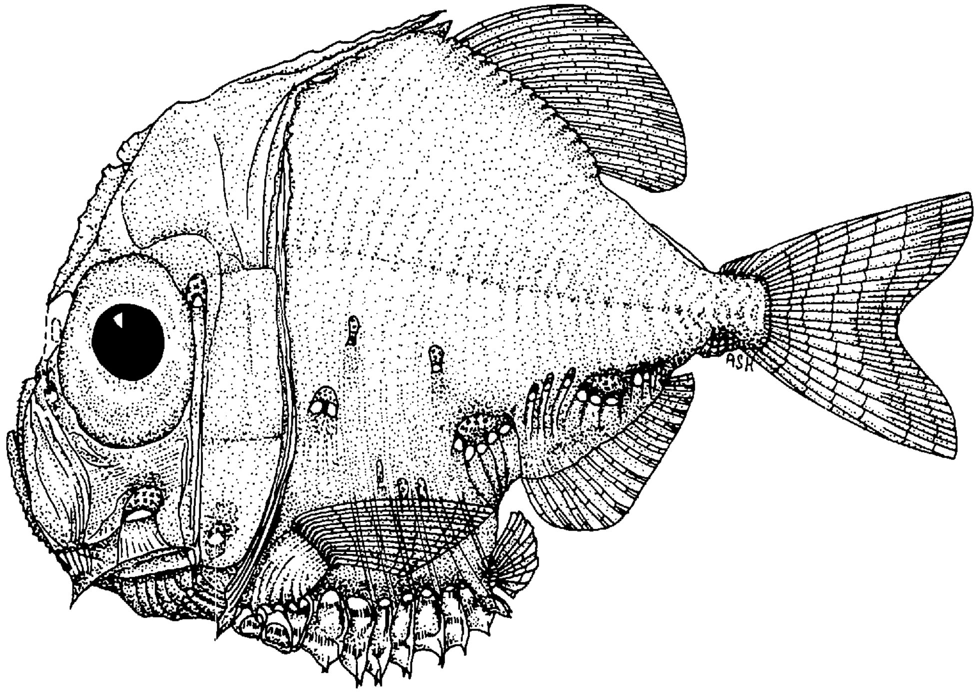

Figure 52. *Polyipnus oluolus*, holotype, USNM 204390, 26.9 mm. Head position and fins reconstructed.

and partially concealed by a field of deep spinelike serrations. The holotype has only 14 anal-fin rays which contrasts with a total range of 15 to 17 for the other three species.

The feature that distinguishes *P. oluolus* from all other members of the *spinosus* species group is the lack of connection between the posteriormost ACA photophore and the anteriormost of the ACB photophores. *Polyipnus oluolus* is also the only species with triangular bladelike extensions of the ventral margins of the PV photophore scales. Some specimens of *P. nuttingi* have PV #9 and #10 scale morphology similar to that of *P. oluolus* but the remaining scales have the rectangular form.

Distribution.—The holotype was collected off the Marshall Islands, depth of capture not known (Fig. 43). No other *Polyipnus* have been reported from this island group.

Remarks.—*Polyipnus oluolus* is known only from the holotype which is in very poor condition. The drawing which appears in Baird's paper (1971: fig. 67) is inaccurate, showing the pectoral-fin base anterior to the position of the cleithrum. An attempt, therefore, was made to reconstruct the original appearance of the holotype in Figure 52, illustrating at least the salient features of this unusual species. Greatest inaccuracy in the drawing is likely to be in the attitude of the head which, in the specimen, is nearly free of the vertebral column.

Characters of the posttemporal and associated spines are critical for identification of *Polyipnus* species and for reconstructing their phylogenetic relationships. It is important to note that the holotype of *P. oluolus* has two posttemporal spines,

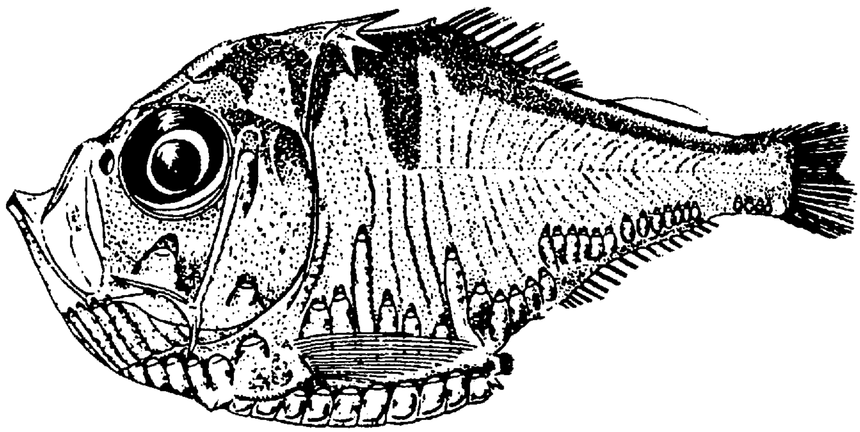

Figure 53. *Polyipnus parini*, holotype, ZIL 43997, 61.0 mm. Reproduced with permission, from Borodulina (1979).

one large and dorsal and another much smaller and basal. This was not made clear in the original description.

Polyipnus parini Borodulina, 1979
Figure 53

Polyipnus parini Borodulina, 1979: 4–6 (holotype fig. 3); 1981: 124.—Fujii, 1984: 47 (pl. 491).—Harold, 1989: 874–875; 1990b: 515.
Polyipnus cf. *parini*.—Borodulina, 1979: 4–6.

Type Material.—Holotype: ZIL 43997 (1, 61.0 mm) (x-radiograph only).

Other Material.—ZIL 43998 (1, 28.0) (x-radiograph only).

Diagnosis.—Autapomorphies: Gill rakers 28 or 30. Posttemporal spines 3, subequal, tridentlike but relatively short: dorsal spine 9.6–12.6% SL. Other characters, in combination: Lateral pigment bar tapered and long, terminating at or near lateral midline. Photophore scale denticles, restricted to PV, VAV and ACB clusters. ACB 10–11, with a gap about equal to the width of one photophore between #3 and #4.

Description.—Maximum adult body size 61.0 mm SL (holotype). D (13) 12. A (17) 17. P (14) 16. V (7). GR (28) 30. Vertebrae (35) 35.

Ventral margins of photophore scales smooth, except as noted below. Photophore counts: OVB 1 + 1 + 1, in an anteriorly-inclined straight line. PV and VAV scales. ACA 1 + 1 + 1, separate, not united in a common organ, aligned with first three ACB photophores. ACA #3 united with ACB #1 forming a continuous organ. ACB (10; 11), with a dorsal step and a broad gap about equal to the width of one photophore between #3 and #4; ACB scales #2 and #3 each with a single denticle (holotype). ACC compact.

Similar Species.—*Polyipnus parini* is most similar to *P. inermis*. These two species have tridentlike posttemporal spine groups and a unique broad gap between photophores #3 and #4 of the ACB cluster. *Polyipnus parini* has a greater number of gill rakers on the first arch than *P. inermis* (28/30 as compared with 23–26). Generally *P. parini* is much more "spiny," with serrated posttemporal keels and denticles on VAV and ACB photophore scales.

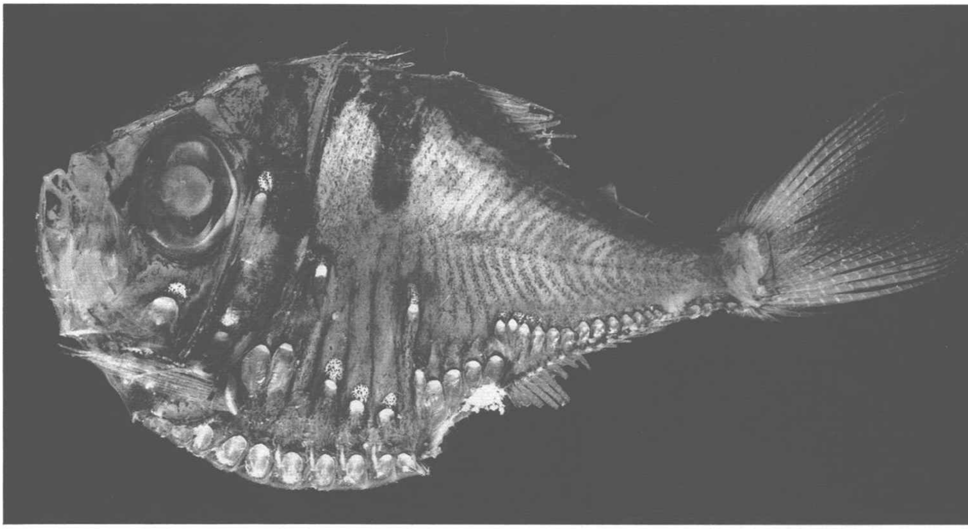

Figure 54. *Polyipnus paxtoni*, paratype, AMS I.25825-002, 45.1 mm.

Distribution.—The geographical distribution of *P. parini* is very poorly known. In the original description Borodulina (1979: 4) says that the holotype was given to the USSR Academy of Sciences with some specimens of *P. matsubarai*. The collection was not labelled but A. S. Sokolvskiy, who donated the specimens conveyed that "they were caught at different times in the 'zone of the Kuroshio Current'" (20–43°N 138–152°E). Aizawa (pers. comm.) is of the opinion that *P. parini* has never been collected near Japan. Nevertheless, a tentative collecting locality is given in Figure 50 which follows the original description (Borodulina, 1979: fig. 2). The only other reported capture of this species (*P.* cf. *parini*, Borodulina, 1979: 5) is in the Tasman Sea off the North Island of New Zealand. Therefore, in the presence of these sparse and ambiguous data, *P. parini* is here considered a western Pacific species.

Remarks.—Unfortunately, neither of the specimens of *P. parini* were available for direct study. Comments made here are derived from the original description with its illustration (Borodulina, 1979) and x-radiographs of both specimens.

On the basis of morphology the "juvenile" small specimen (ZIL 43998, 28.0 mm SL) referred to *P.* cf. *parini* by Borodulina (1979: 4–6) is not distinguishable from the holotype. From her discussion it appears that the source of doubt regarding the identification of this juvenile specimen was the "considerable separation" of the collecting localities. The specimen is treated here as a valid representative of *P. parini*.

The diagnosis and description provided by Borodulina (1979) are in one aspect contradictory. In the diagnosis the "anal" (ACB) photophores are described as being without "spiny scales" but in the description such spines (=denticles) are present albeit restricted to photophores #2 and #3 of the cluster.

Polyipnus paxtoni Harold, 1989
Figure 54

Polyipnus paxtoni Harold, 1989: 871–876 (holotype fig. 1).

Type Material.—Holotype: AMS I.25825-009 (1, 42.5 mm). Paratypes: AMS I.25825-002 (7, 41.8–49.3 mm). AMS I.25816-006 (3, 41.6–46.3 mm).

Diagnosis.—Autapomorphies: Anal-fin pterygiophores number 7 and 8, those immediately anterior to anal-fin hiatus, and those immediately posterior, numbers 9 and 10, are fused. Denticles of ACB photophores well-developed, extending from diagonal flanges of modified, covering scales. First infrapharyngobranchial subcylindrical, not posteriorly expanded. Other characters, in combination: Gill rakers 23 or 24. Lateral projection of dark pigment tapered and long, reaching lateral midline. Three posttemporal spines present, dorsal spine longest, median and ventral spines subequal and about ¼ to ½ of length of dorsal spine. Numerous denticles originating on scales of PV, VAV, ACB, ACC and occasionally ACA #3 photophores. ACB 10–12. ACC compact.

Description.—Maximum adult body size moderate, up to 49.3 mm SL. D (12) 11–13. A (17) 15–18. P (12) 12/13. V (7) 7. GR 7/8 + 16/17 = (23) 23/24. Vertebrae 33–35.

Ventral margins of photophore scales smooth, without denticles, except as noted below. OVB 1 + 1 + 1, in an anteriorly-inclined straight line. PV and VAV ventral scale margins with numerous denticles. ACA 1 + 1 + 1, in a straight line, #3 united with ACB #1, forming a continuous organ. ACA #3 frequently with denticulate ventral margin. ACB (11; 10–12), with an indistinct dorsal step between #3 and #4; most scales with five or more denticles ventrolaterally, often originating on diagonal scale flange. ACC compact, denticulate, scales extending ventrally beyond body outline.

Similar Species.—All species of the *P. spinosus* species group have three posttemporal spines except *P. nuttingi, P. asper* and *P. oluolus,* which have one large dorsal and one small ventral spine with a series of associated deep spinelike serrations, and *P. indicus* which usually has two and occasionally three spines. *P. paxtoni* differs from *P. indicus, P. oluolus, P. tridentifer, P. stereope, P. spinosus, P. elongatus, P. soelae* and *P. inermis,* in having denticles over most scales of the ACB photophore cluster. Denticles are present in the ACB cluster of *P. parini,* but are apparently restricted to the second and third scales. *Polyipnus tridentifer* and *P. soelae* may in large specimens have a single weak denticle on some of the ACB photophore scales. *Polyipnus fraseri,* has numerous denticles on all ACB photophore scales but there are only four organs in the cluster. *P. paxtoni* is similar to *P. spinifer,* in denticulation but differs in having equidimensional ventral and median posttemporal spines, a long, tapered lateral dark pigment bar that reaches the lateral midline and usually 11 (10–12) AN photophores (11–13 in *P. spinifer*). One other species, *P. asper,* has denticulate ACB photophores but unlike *P. paxtoni* has two posttemporal spines and 8–10 ACB photophores. *P. paxtoni* is similar to *P. elongatus* with regard to pigmentation and posttemporal morphology.

Distribution.—*P. paxtoni* is known only from two SOELA stations in the Coral Sea, off the north-east coast of Queensland, Australia, at about 18°S latitude, 147°E longitude (Fig. 46). The specimens were taken between the surface and a depth of 300 m at night.

The geographic range of *P. paxtoni* appears to overlap to some degree that of *P. elongatus, P. triphanos, Polyipnus* sp. B, and possibly *P. aquavitus.* On the basis of the few captures, *P. paxtoni* and *P. elongatus* are endemic to the Coral Sea but may not occupy the same geographic or bathymetric areas within the region. Numerous trawl samples from other parts of the Coral Sea that contained other *Polyipnus* species (*P. aquavitus* and *P. unispinus*) indicate that *P. paxtoni* (and *P. elongatus*) may be restricted to the western Coral Sea off Queensland.

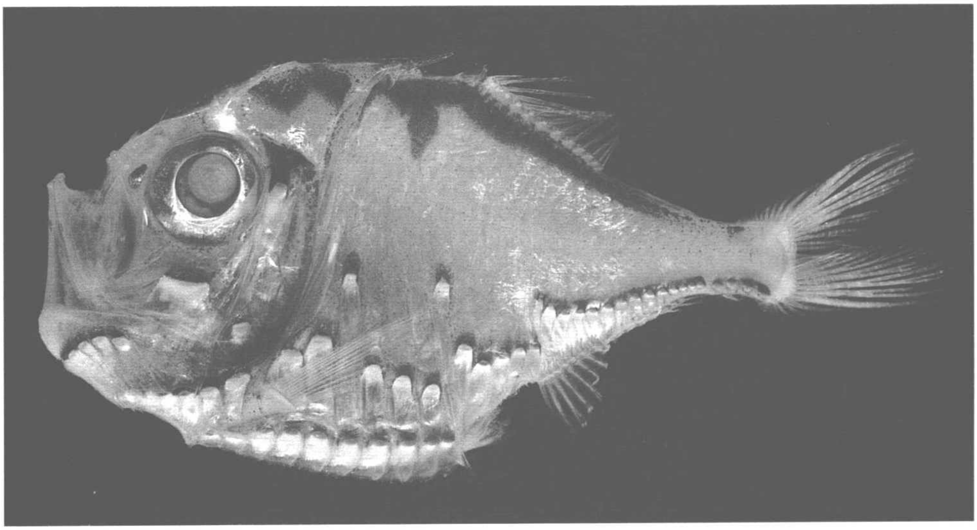

Figure 55. *Polyipnus soelae*, holotype, AMS I.22808-028, 54.8 mm.

Remarks.—*Polyipnus paxtoni* is a recent addition to the genus (Harold, 1989). Posttemporal morphology is quite similar to that of *P. elongatus*. The rudimentary median and ventral posttemporal spines in both species are virtually concealed by adjacent spinelike serrations. Unlike serrations, the spines originate medially at the base of the dorsal spine and are joined by an ossified sheet. In spite of posttemporal similarities, *P. paxtoni* and *P. elongatus* are very distinct with regard to scale denticulation, various fin-ray and photophore meristic characters and body shape.

Polyipnus soelae new species
Figure 55

Polyipnus spinosus.—Brauer, 1906: 120, 376.—Misra, 1976: 241–243 (part).—Borodulina, 1979: 7–9 (part).—Paxton et al., 1989: 192 (part).
Polyipnus spinosis.—Borodulina, 1979: 7 (incorrect subsequent spelling of *P. spinosus*).
Polyipnus spinifer.—Harold, 1990b (part, AMS I.22808-028 and I.22817-014).

Type Material.—Holotype: AMS I.22808-028 (1, 54.8 mm), 17°59'N 118°17'E, (0–) 404–420 m, 0550–1400 h, SOELA, field no. SO 2-82-17, 18, 3 Apr 1982. Paratypes: AMS I.22808-[028] (29 of 30 from AMS I.22808-028, 38.5–52.1 mm), same data as holotype. AMS I.22817-014 (30, 49.6–60.1 mm), 18°06'S 117°45'E, (0–) 492–520 m, 0555–1450 h, SOELA, field no. SO-2-82-31,32,33,34, 7–10 Apr 1982. IOAN uncat. (15, 41.4–50.2 mm), 09°06'S 131°15'E, 0–340 m, VITYAZ, trawl 37.1, 26 May 1967.

Other Material.—AMS I.23423-001 (5, 38.3–50.7 mm), 18°01'S 118°23'E, 0–376 m, SOELA, 1 Aug 1982. AMS I.23425-011 (8, 40.4–43.0 mm), 18°46'S 117°00'E, 0–400 m, SOELA, 1 Aug 1982. FMNH 52447 (1, 46.7 mm), 07°15'S 115°15.6'E, SIBOGA Sta. 12, 14 Mar 1899. IOAN uncat. (7, 29.5–43.2 mm), 09°05'S 131°22'E, 0–316 m, AKADEMIK BERG, 19 Jul 1967. IOAN uncat. (1, 47.7 mm), 09°00'S 130°39.8'E, 445–520 m, AKADEMIK BERG, 30 Oct 1968. USNM 135537 (5, 49.2–57.6 mm), 00°07'30"N 127°29'E, ALBATROSS Sta. D5626, 29 Nov 1909. WAM P26209-010 (3, 46.0–53.0 mm), 18°18'S 118°08'E, 297–330 m, COURAGEOUS, 20 May 1978. WAM P27612-004 (3, 25.0–28.0 mm), 18°33'S 121°01'E, COURAGEOUS, trawl 49-1086, 19 May 1979. WAM P28057-007 (2, 50.0–53.0 mm), 18°05'S 118°06'E, (0–) 432 m, 17 Aug 1983.

Diagnosis.—Autapomorphies: Incision of maxillary ventral margin for premaxillary attachment absent. Basisphenoid posterior spinelike process highly elongate.

Median flanges of posterior anal-fin proximal radials narrow proximally. Mesopterygoid pitting reduced to absent. Other characters, in combination: Gill rakers 20–23. Lateral pigment bar short and triangular, reaching about half way to lateral midline. Predorsal and postdorsal pigment notches absent. Three posttemporal spines: dorsal spine longest, median spine shortest, ventral spine with a slight anterior arc. Photophore scale denticles mainly restricted to PV, VAV and ACC clusters but ACB scales may have a single weak denticle in specimens over 50 mm SL. ACB 11–14. ACC photophore reflectors separated by large gaps.

Description.—Maximum adult body size moderate, up to 60.3 mm SL. D (13) 12–14. A (16) 15–17. P (13) 12–13. V (7) 7. GR 5–7 + 13–16 = (21) 20–23. Vertebrae (34) 33–35. Body profile anterior of dorsal fin broadly elliptical. Caudal peduncle rectangular, highly elongate. Ventral margin of dentary with two parallel serrate keels. Margins of dentary and premaxilla with minute, recurved teeth. Maxilla with smaller, conical teeth. Anterior region of vomer with a transverse patch of 12 to 16 longitudinal rows of minute conical teeth. No teeth present on posteromedian process of vomer. Two or three conical teeth in a median row on palatine. Frontal and parietal keels serrate. Parietal keel discontinuous; posterior region with two minute conical spines, directed anteriorly and posteriorly. Limbs of posttemporal each with two lateral serrate keels. Posttemporal with three posterolaterally-directed spines: dorsal spine longest (7.4–16.9% SL), ventral spine shorter (3.3–6.7% SL), median spine less than one half of the length of the dorsal spine. Ventral margin of pectoral shield with 6–13 minute conical spines. Vertical and anteroventral rami of preopercle each with two parallel lateral ridges, ventral ridge of anteroventral ramus usually with one to three serrations. Preopercle with two spines: ventral spine long (7.1–12.3% SL), slightly curved distally toward anterior and axis of spine directed ventrally; dorsal spine minute (slightly longer than one preopercular serration), conical and directed ventrolaterally. Dorsal spinous process short-based, exposed length and height about equal, anterodorsal surface blade-like with one or two deep spine-like serrations, terminating posteriorly in two elongate conical spines, one per side, directed dorsolaterally. Anal-fin pterygiophore spines absent.

Morphometric characters (% SL): Head length 30.1–30.8, orbit length 13.1–18.8, body depth 56.7–64.9, caudal-peduncle depth 9.3–12.8, caudal-peduncle length 15.1–22.3, dorsal-fin length 17.4–23.3, anal-fin length 20.3–27.0, preanal length 65.0–75.5, predorsal length 52.5–65.2, preventral length 58.6–74.6, postdorsal length 49.7–63.0, postanal length 36.6–48.7, ACC length 7.4–11.5, ACB-C length 0.2–2.3.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. OVB 1 + 1 + 1, in an anteriorly-inclined straight line. Ventral margins of PV and VAV scales with numerous denticles. ACA 1 + 1 + 1, in a straight line and appearing continuous with ACB cluster, ACA #1 and #2 isolated, not connected to each other or to #3 by a lumen; #3 connected to ACB forming a continuous organ. ACB (11; 11–14), with an indistinct dorsal step between #3 and #4; nondenticulate ventral scale margins except in specimens larger than 50 mm SL which occasionally have one weak denticle per scale. ACC scales with ventral lamellae extending beyond lateral outline and numerous but often weak denticles.

Dark pigment saddle present: predorsal and postdorsal notches generally absent, but minute predorsal inflection of pigment margin occasionally present. Lateral projection short, triangular, ventrally-tapered and extending about half way to the

lateral midline. Generally flank appears unpigmented and contrasts sharply with the dorsal region of the body.

Similar Species.—*Polyipnus soelae* is most similar to *P. spinifer* and *P. tridentifer*; distinguished from *P. spinifer* mainly by a lack of denticles on the ACB photophore scales and from *P. tridentifer* by its reduced median and ventral posttemporal spines. See also Similar Species section for *P. spinifer* and *P. tridentifer.*

Distribution.—*Polyipnus soelae* occurs off the northwest coast of Australia (Indian Ocean) and in the Timor, western Arafura, Celebes, and Madura Seas of Indonesia (Fig. 45). References to *P. spinosus* from peninsular India in Baird (1971) may represent *P. soelae.* The bathymetric range is about 520 m maximally to about 300 m.

The geographic range of *P. soelae* does not appear to overlap with either of the most closely related species *P. spinifer* (Philippine and Japanese Archipelagos) and *P. tridentifer* (Great Australian Bight). There is, however, possible overlap with *P. spinosus* to the south of the Philippines. More distantly related congenerics (not members of the *P. spinosus* species group) occurring within the range of *P. soelae* include *P. meteori, P.* aff. *kiwiensis, P. triphanos, P. unispinus, P. aquavitus,* and *P. omphus.*

Remarks.—Although *P. soelae* is nearly identical in its most obvious external features to *P. spinifer* it has been misidentified as *P. spinosus* in the literature (Borodulina, 1979: 7–8; Paxton et al., 1989: 192). The redescription of *P. spinosus* provided by Borodulina (1979) was based upon erroneously identified Russian collections of "*P. spinosus*" (=*P. soelae*) and not the holotype. In her key to the species of the "*P. spinosus* subgroup," the type species *P. spinosus* sensu stricto cannot be identified. The description and key indicate that the subcaudal photophores (=photophore scales) of *P. spinosus* are "spinous" (=denticulate) but it is not true of the holotype (pers. obs.; Bourret, 1985) or of the additional specimen reported here.

Etymology.—Named for the Australian vessel SOELA from which many specimens of *P. soelae* were collected.

Polyipnus spinifer Borodulina, 1979
Figure 56

Polyipnus spinosus.—Schultz, 1938: 143–144 (part).—Matsubara, 1950: 187–197 (fig. 2; fig. 4A, photophore scale denticles, part).—Okada and Suzuki, 1956: 296–302 (fig. 1, part).

Polyipnus tridentifer.—Schultz, 1961: 646–647 (part).—Baird, 1971: 86–88 (fig. 64, part).—Weitzman, 1974: 345.

Polyipnus spinifer Borodulina, 1979: 6–7 (holotype fig. 4).—Fujii, 1984: 47 (pl. 49J).—Bourret, 1985: 59–61.—Harold, 1989: 871–876; 1990b: 515 (part).

Type Material.—Holotype: ZIL 43996 (1, 59.0 mm) (not available for direct study; x-radiograph provided by A. P. Andriashev, ZIL). Paratypes: ZIL 43995 (4, 45.0–51.0 mm) (x-radiographs only).

Other Material.—AMS I.B4604 (1, 52.1 mm). AMS I.B4605 (1, 48.2 mm). AMS I.B4606 (1, 44.8 mm). CAS 32254 (1, 58.0 mm). CAS 34854 (6, 48.6–51.5 mm). IOAN uncat. (1, 51.0 mm), 30°50′N 127°49′E to 30°48′N 127°46′E, 150–0 m, VITYAZ Cr. 22, Sta. 3541, 0042–0153 h, 02 Nov 1955. MNHN 1984-375 (2, 50.0–54.0 mm). MNHN 1984-377 (1, 60.0 mm). MNHN 1984-378 (17, 34.0–58.0 mm) ORIT 2551, 2554, 2557–2568 (14, 38.4–49.0 mm). USNM 103036 (2, 47.6–49.1 mm). USNM 103044 (1, 38.5 mm). USNM 135514 (4, 45.0–56.3 mm). USNM 135523 (4, 44.9–47.0 mm). USNM 135525 (1, 36.9 mm). USNM 135528 (11, 30.9–54.8 mm). USNM 135535 (39, 39.3–56.4 mm). USNM 135536 (13, 58.9–44.5 mm). USNM 289176 (3, 22.9–25.6 mm). ZMUC C.N. 3 (1, 54.0 mm).

Diagnosis.—Autapomorphy: Photophore scale denticles large and perfuse on PV,

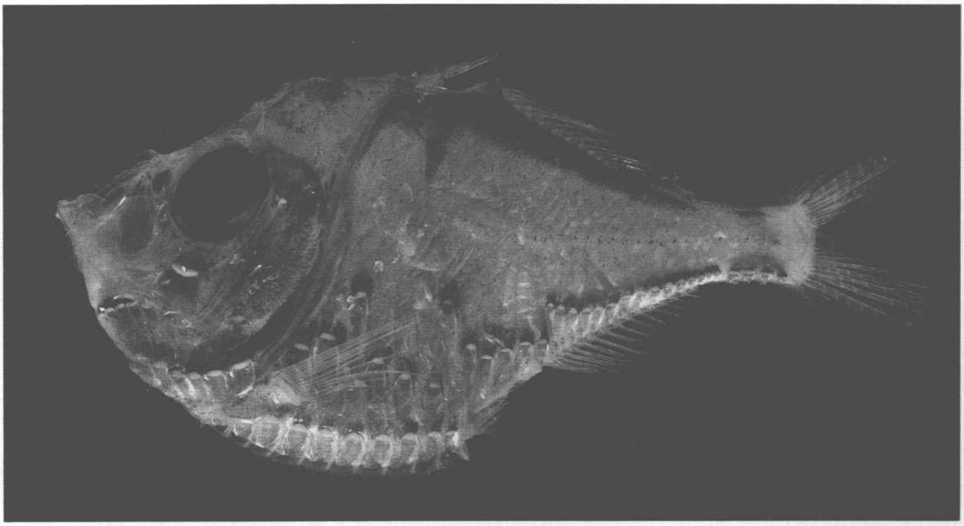

Figure 56. *Polyipnus spinifer,* ORIT 2565, 38.7 mm.

VAV, ACB and ACC clusters (homoplastic). Other characters, in combination: Gill rakers 19–25. Lateral pigment bar short and triangular, reaching about half way to lateral midline; without dorsal deflections of pigment margin posterior of projection. Three posttemporal spines: dorsal spine longest (9.3–16.8% SL), median spine shortest and ventral spine intermediate and with a slight anterior arc. ACB 11–13. ACC photophore reflectors separated by large gaps.

Description.—Maximum adult body size moderate, up to 52.1 mm SL, reported to 60.0 mm (Borodulina, 1979: 6). D (13) 12–14. A (16) 15–18. P (13) 12–14. V (7) 7. GR 6–8 + 13–16 = 19–24 (21–25 for type series, Borodulina, 1979). Vertebrae (34) 33–35.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. OVB 1 + 1 + 1, in an anteriorly-inclined straight line. PV and VAV scale ventral margins with spine-like denticles. ACA 1 + 1 + 1, in a straight line and appearing continuous with ACB photophores: #1 and #2 isolated, not connected to each other or to #3 but the latter connected to first ACB forming a continuous organ; ACA #3 frequently with denticulate ventral margin. ACB (12; 11–13), with an indistinct dorsal step between #3 and #4; most scales with five or more denticles. ACC scales with ventral lamellae extending beyond ventral outline and numerous denticles.

Similar Species.—*P. spinifer* is most similar to *P. tridentifer* and *P. soelae,* and bears some resemblance also to *P. inermis, P. parini, P. spinosus, P. stereope.* These species have in common three large subequal posttemporal spines. Of these, only *P. spinifer, P. soelae* and *P. tridentifer* have denticulate ACC photophore scales. *P. spinifer* differs from the latter two species by the presence of multiple denticles on scales of the ACB photophores.

Distribution.—*P. spinifer* is known from Suruga Bay, Japan, the East China Sea and off the Philippines in the South China and Sulu Seas (Fig. 45). The bathymetric range is generally about 220 m to 380 m but specimens have been taken above 150 m in Suruga Bay, Japan.

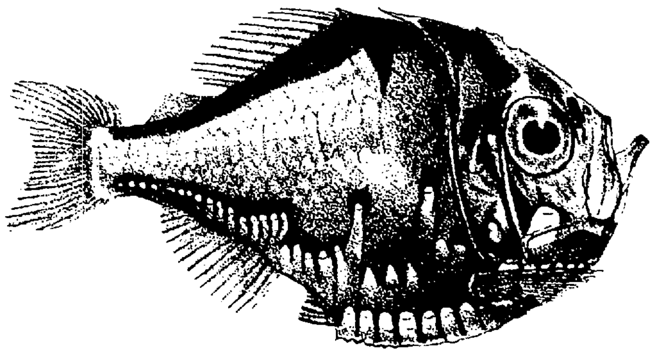

Figure 57. *Polyipnus spinosus,* holotype, BMNH 1987.12.7.159. After Günther (1887).

To the south of the Philippines, the geographic range of *P. spinifer* meets and possibly overlaps that of *P. soelae* and *P. spinosus* of the members of the *spinosus* group. The range clearly overlaps that of *P. stereope* around the Japanese Archipelago. Other species possibly occurring within the range of *P. spinifer* include *P. fraseri, P. matsubarai, P. meteori, P. ovatus, P. triphanos, P. danae* and *P. unispinus.*

Remarks.—Populations of *P. spinifer* (East China Sea and Philippines) have in the past been considered to be *P. tridentifer* (Baird, 1971; Schultz, 1961) or *P. spinosus* (Schultz, 1938; Matsubara, 1950; Okada and Suzuki, 1956). Borodulina (1979) established that these northern populations are distinct at the species level from *P. tridentifer* (Great Australian Bight). Specimens from Indonesia and off the northwest coast of Australia are nearly indistinguishable from *P. spinifer* but have in the past been referred to *P. spinosus* (Borodulina, 1979: 7). Such specimens are here described as a new species, *P. soelae.* See Remarks section for *P. soelae* and *P. tridentifer.*

Polyipnus spinosus Günther, 1887
Figure 57

Polyipnus spinosus Günther, 1887: 170 (holotype pl. 5, fig. 1B).—Goode and Bean, 1896: 128 (pl. 39, fig. 148).—Garman, 1899: 238.—Gilbert, 1905: 609–610.—Brauer, 1906: 120, 376 (part).—McCulloch, 1914: 89.—Fowler, 1936: 240–241 (part).—Parr, 1937: 55.—Schultz, 1938: 142–144 (part).—Matsubara, 1950: 188–192 (part, fig. 2 is *P. spinifer* Borodulina, 1979).—Okada and Suzuki, 1956: 296–302 (part).—Baird, 1971: 89–90.—Misra, 1976: 241–243 (part, fig. 66, after Brauer, 1906, is probably *P. soelae* or *P. spinifer*).—Borodulina, 1979: 7 (part, *P. spinosus* Günther, 1887 in synonymy; remaining description refers to *P. soelae* n. sp.).—Bourret, 1985: 59–61.—Paxton et al., 1989: 192 (part).—Harold, 1989: 874–875; 1990b: 515.

Polyipnus spinosus spinosus.—Schultz, 1961: 647–649 (holotype fig. 24); 1964: 268.

Polyipnus spinosis (sic).—Borodulina, 1979: 7 (incorrect subsequent spelling; part, Günther, 1887 only).—Yamamoto, 1982: 327.

Type Material.—Holotype: BMNH 1987.12.7.159 (1, 45 mm).

Other Material.—LACM 36062 (1, 23.5 mm).

Diagnosis.—No autapomorphies found; diagnosed by the following characters in combination. Gill rakers 19–21. Lateral pigment bar tapered and moderately long, approaching but not reaching lateral midline. Three posttemporal spines: dorsal longest, median spine shortest; length of median and ventral spines less than or equal to half that of dorsal spine. Photophore scale denticles restricted to PV and

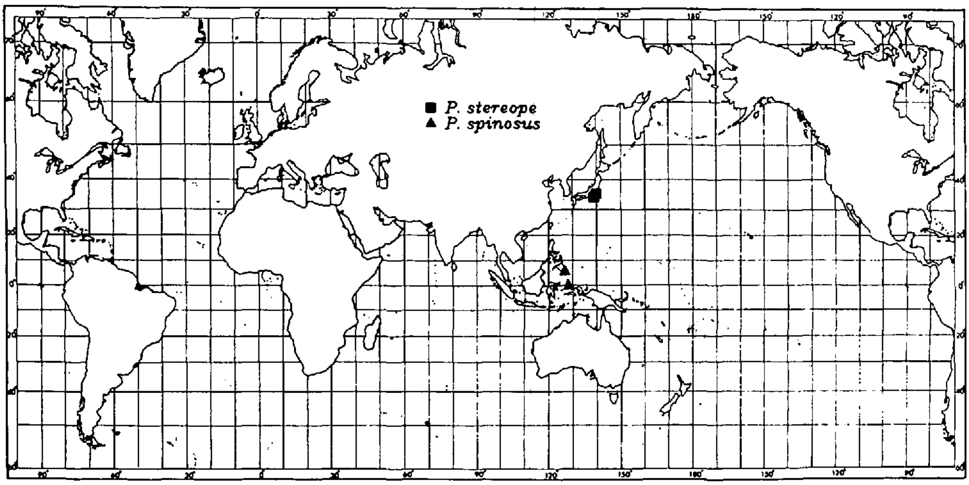

Figure 58. Collection station localities for *P. stereope* and *P. spinosus*, *P. spinosus* species group.

VAV clusters. ACB (9–11). ACC photophores compact. Palatine teeth absent. Caudal peduncle deep and slightly tapered posteriorly.

Description.—Maximum adult body size moderate, up to 85 mm SL. D (12) 12–14. A (15) 15–17. P (14) 12–13. V 7. GR 5/6 + 13 = (19/18) 19–21 (20 and 21 according to Bourret, 1985: 59). Vertebrae (32) 32/33 (33 according to Bourret, 1985).

Ventral margins of all photophore scales smooth, without denticles, except as noted below. OVB 1 + 1 + 1, in an anteriorly-inclined straight line. PV and VAV scale ventral margins with numerous denticles. ACA 1 + 1 + 1, in an anteriorly-inclined straight line: #1 and #2 isolated, not visibly connected to each other or to #3 by a lumen; #3 connected to ACB forming a continuous organ. ACB (10), with an indistinct dorsal step between #3 and #4. ACC compact, scales with extensive flangelike ventral margins extending beyond ventral profile but without denticles.

Similar Species.—*P. spinosus* is similar to *P. stereope, P. spinifer, P. soelae, P. tridentifer, P. parini, P. inermis,* and *P. fraseri* with regard to posttemporal morphology (all have three large posteriorly-directed spines). Other species that have three posttemporal spines have reduced equidimensional ventral and median spines (*P. paxtoni* and *P. elongatus*). *Polyipnus spinosus* is distinguished from *P. tridentifer, P. spinifer, P. soelae* and *P. fraseri* by its lack of denticles on the ventral margins of the ACC photophore scales and from *P. parini* and *P. inermis* by the lack of a large gap between photophores ACB #3 and #4. *P. spinosus* is most similar to *P. stereope* in body shape and pigmentation pattern, however the former has fewer gill rakers (18–21, as compared with 22–28 in *P. stereope*) and lacks palatine teeth.

Distribution.—*Polyipnus spinosus* is known from the Celebes and Halmahera Seas and from around the Philippine Islands (Fig. 58). Schultz (1961) also listed the Bay of Bengal and the east coast of Africa as part of the geographic range but this cannot now be confirmed by examination of specimens. The USNM collections that Schultz (1961: 648) refers to have been lost through loan trans-

actions. I suspect that material from the African coast is *P. indicus* and from the Bay of Bengal either *P. soelae, P. asper,* or an undescribed species.

Schultz (1961) gives a bathymetric range of 185 to 561 m but being based on open tows the 561 m should be regarded as a maximum possible, not an actual depth of capture. The holotype was taken between the surface and 472 m and data from one discrete-depth sample examined here (ALPHA HELIX Sta. 128) gives a range of 350–390 m.

There is range overlap between *P. spinosus* and *P. soelae, P. meteori, P. triphanos, P. aquavitus, P. unispinus* and possibly *P. omphus. Polyipnus spinosus* was taken in the same tow as *P. aquavitus* at ALPHA HELIX Sta. 128.

Remarks.—The most similar species to *P. spinosus* and one that has been thought synonymous by some investigators (Matsubara, 1950) is *P. stereope.* Schultz (1961) recognized both forms but only as subspecies of *P. spinosus* (i.e., *P. spinosus spinosus* and *P. spinosus stereope*). Baird (1971) recognized these similar but distinct forms as species and they are treated as such here.

In her account of *P. spinosus,* Borodulina (1979: 7) notes that two important diagnostic features are a long and narrow caudal peduncle and "spinous" (=denticulate) scales on the subcaudal (=ACC) photophores. Neither of these features are found in the holotype or the other specimen examined here (LACM 36062). Re-examination of some of the specimens ascribed to *P. spinosus* by Borodulina has shown them to be representatives of another species (*P. soelae* n. sp.), related to *P. spinifer* and *P. tridentifer.*

The lack of autapomorphies for this species is likely the result of unavailability of specimens for internal osteological study.

Polyipnus stereope Jordan and Starks, 1904
Figure 59

Polyipnus stereope Jordan and Starks, 1904: 581 (holotype pl. 2, fig. 3).—Gilbert, 1905: 609–610.—McCulloch, 1914: 89.—Okada and Suzuki, 1956: 296–302.—Borodulina, 1979: 7.—Fujii, 1984: 47 (pl. 49K).—Bourret, 1985: 59–61.—Harold, 1989: 871–876; 1990b: 515.

Polyipnus spinosus.—Schultz, 1938: 143–144 (part).—Matsubara, 1950: 189 (part).

Polyipnus sterope (sic).—Schultz, 1961: 636, 637 (table 6).—Baird, 1971: 88–89 (incorrect subsequent spelling).

Polyipnus spinosus stereope.—Schultz, 1961: 649 (holotype fig. 25); 1964: 268.

Type Material.—Holotype: USNM 051451 (1, 51.7 mm). Paratype: USNM 177895 (1, 24.2 mm).

Other Material.—NSMT P.6773 (1, 38.5 mm). ORIT 2519 (1, 47.5 mm).

Diagnosis.—Autapomorphies: Lateral pigment bar is highly tapered and moderately long, approaching but not reaching lateral midline. Caudal peduncle stout, about as deep as long, slightly tapered posteriorly. Other characters, in combination: Gill rakers 22–28. Three posttemporal spines: dorsal longest (8.5–8.8% SL), median spine shortest; length of median and ventral spines less than or equal to half length of dorsal spine. Anal-fin pterygiophore spines absent. Photophore scale denticles restricted to PV and VAV clusters. ACB (9–11). ACC photophores compact. Three or four palatine teeth.

Description.—Maximum adult body size moderate, up to 51.7 mm SL (holotype). D 13–14. A 15–16. P 13–16. V 7. GR 7–10 + 15–18 = (23) 22–28. Vertebrae (33) 33.

Ventral margins of all photophore scales smooth, without denticles, except as noted below. OVB 1 + 1 + 1, in an anteriorly-inclined straight line. PV and VAV scale ventral margins with spinelike denticles. ACA 1 + 1 + 1, in an

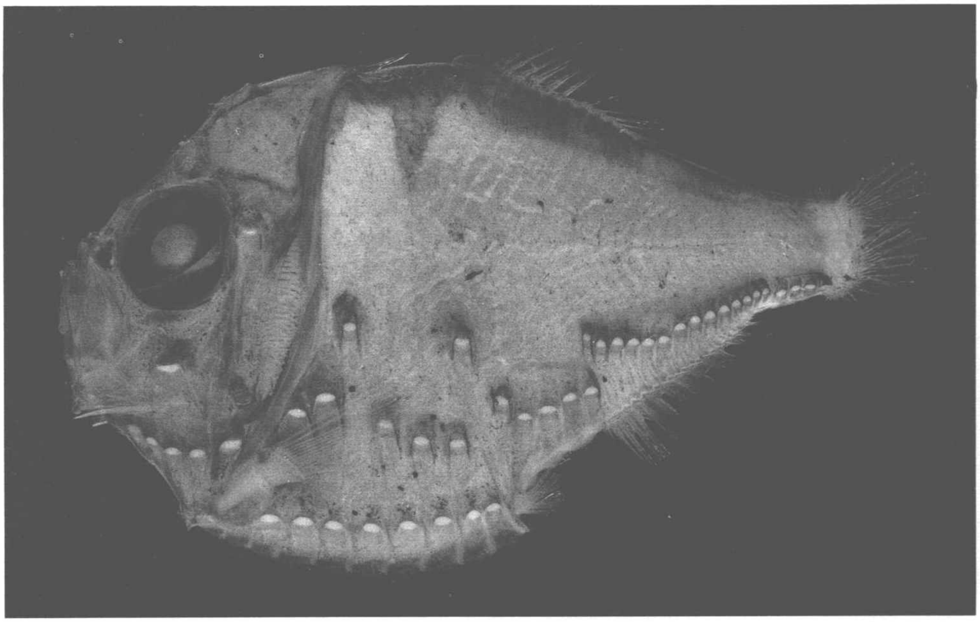

Figure 59. *Polyipnus stereope*, ORIT 2519, 47.5 mm.

anteriorly-inclined straight line: #1 and #2 isolated, not connected to each other or to #3 by a lumen; #3 connected to first ACB, united in a continuous organ. ACB (10; 9–11), with an indistinct dorsal step between #3 and #4. ACC compact, scales without extensive flangelike ventral margins extending beyond ventral profile.

Similar Species.—*P. stereope* is most similar to *P. spinosus* with regard to most meristic characters and body shape. These are the only *Polyipnus* species with a deep, posteriorly-tapered caudal peduncle. These species also have nondenticulate scales covering the ACB and ACC photophores. The only other species with this combination is *P. inermis* which is otherwise distinguished by a large step and a break in the ACB photophores, body shape and posttemporal features. *P. stereope* is distinguished from *P. spinosus* on the basis of larger number of gill rakers (22–28 as compared with 19–21) and presence of palatine teeth.

Distribution.—*P. stereope* is restricted to the seas around Japan: East China Sea and Suruga and Sagami Bays (Fig. 58) at depths of about 150 to 280 m.

The geographic range of *P. stereope* overlaps with that of *P. spinifer* (*P. spinosus* species group), *P. matsubarai* (*P. meteori* species group) and *Polyipnus surugaensis.*

Remarks.—*Polyipnus stereope* is most closely related to the Indonesian species *P. spinosus*, both regarded by Schultz (1961) as subspecies of *P. spinosus*. Affinity of the two forms was indicated to Schultz by the robust body and caudal peduncle, as well as the relatively short posttemporal spine[s]. The caudal peduncle of *P. stereope* appears deeper than that of *P. spinosus*, although this is not borne out by the morphometric measurements (12.9–13.0 as compared with 12.7–14.9% SL). The fact that the caudal peduncle of *P. stereope* is more acutely tapered and consequently deeper anterior of the point of measurement explains this discrep-

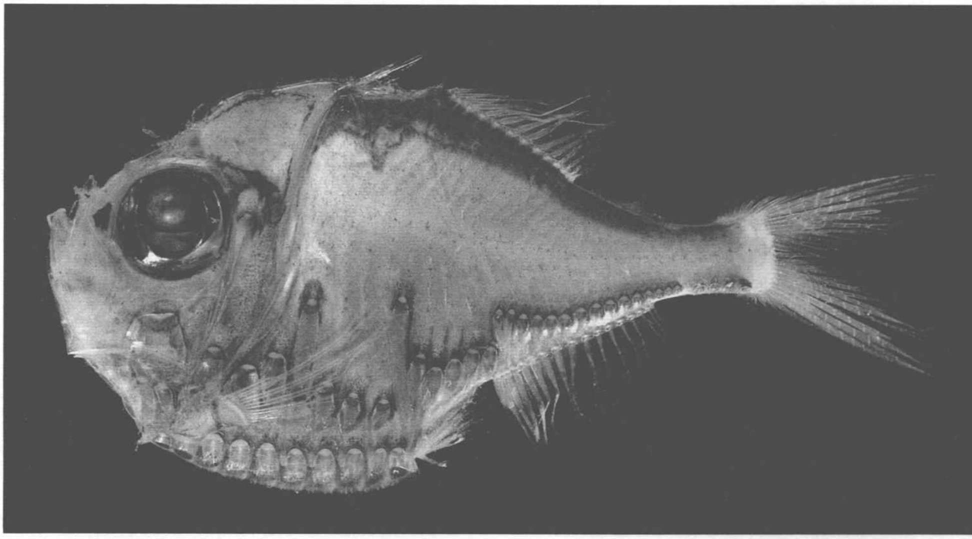

Figure 60. *Polyipnus tridentifer*, AMS I.32134-001, 46.9 mm, paralectotype.

ancy. The marked taper and stoutness of the caudal peduncle in *P. stereope* clearly distinguishes the species from all congenerics.

Polyipnus tridentifer McCulloch, 1914
Figure 60

Polyipnus tridentifer McCulloch, 1914: 87–89; 1929: 51.—Schultz, 1961: 646–647 (fig. 23, part).—Baird, 1971: 86–88 (part).—Borodulina, 1979: 3–4.—Paxton et al., 1989: 192.—Harold, 1989: 871–876; 1990b: 515.
Polyipnus spinosus.—Schultz, 1938: 143–144 (part).—Matsubara, 1950: 189 (part).
Polyipnus trigentifer.—Okada and Suzuki, 1956: 296–302 (incorrect subsequent spelling).

Type Material.—Lectotype: AMS E.3543 (1, 72.1 mm). Paralectotypes: AMS E.3542 (3, 63.1–67.6 mm). AMS I.32134-001 (29, 40.0–74.1 mm). AMS I.32134-002 (3, 67.5–71.6 mm).

Other Material.—AMS E.5687 (1, 67.6 mm). AMS I.18711-014 (7, 48.3–69.3 mm). ZIL 39034 (6 of 9, 29.8–51.5 mm) (x-radiographs only).

Diagnosis.—Autapomorphies: Supraoccipital posteromedian process absent. First infrapharyngobranchial slightly curved and anteriorly expanded. Dorsolateral surface of posttemporal anterior to base of large dorsal spine with several small hook-like spines in large specimens. Proximal radials of dorsal fin lack pitting. Other characters, in combination: Gill rakers 19–25. Lateral pigment bar short and triangular, reaching about half way to lateral midline, without dorsal deflections of pigment margin posterior of projection. Three large subequal posttemporal spines: dorsal spine length 7.4–13.7% SL. Photophore scale denticles mainly restricted to PV, VAV and ACC clusters but ACB scales may have a single weak denticle in specimens over 50 mm SL. ACB 11–14. ACC photophore reflectors separated by conspicuous gaps.

Description.—Maximum adult body size moderate to large, up to 71.6 mm SL, reported to 93.0 mm (McCulloch, 1914: 89). D 13–14. A 17–18. P 12–13. V 7. GR 6–8 + 13–17 = 19–25. Vertebrae 34–35.

Ventral margins of all photophore scales smooth, without denticles, except as

noted below. OVB 1 + 1 + 1, in an anteriorly-inclined straight line. PV and VAV scale ventral margins with spinelike denticles. ACA 1 + 1 + 1, in a straight line and appearing continuous with photophores of ACB cluster: #1 and #2 isolated, not connected to each other or to #3; #3 connected to first ACB, forming a continuous organ. ACB (11–14), with an indistinct dorsal step between #3 and #4, usually not ornamented but large specimens may have a single small denticle on each of the first four scales of the cluster. ACC compact, scales with ventral lamellae extending beyond lateral outline and numerous denticles.

Similar Species.—*P. tridentifer* is most similar to *P. spinifer* and *P. soelae.* These three species have similar counts for fin rays and ACB photophores. Saddle pigmentation is similar in the absence or reduction of the predorsal notch. Also common to this trio of species is a long very narrow caudal peduncle, large gaps between ACC photophores and only a very minute gap between the ACB and ACC clusters. *P. tridentifer* is distinguished from these other two species by a lack of palatine teeth and usually shorter dorsal posttemporal and ventral preopercular spines.

Distribution.—*P. tridentifer* was described originally from material collected in the Great Australian Bight (McCulloch, 1914). Borodulina (1979) has shown that *P. tridentifer* is endemic to the seas off southern Australia (Fig. 45), subdividing the previously widespread species. I have examined no material contradicting Borodulina's result. Bathymetric data (from open bottom trawls) indicate only that the species occurs above 650 m.

No other *P.* species are known from the Great Australian Bight although *P. kiwiensis, P. ruggeri, P. aquavitus, P. unispinus* and *P. parini* occur to the east in the Tasman Sea vicinity and *P. soelae* off the northwestern coast of Australia.

Remarks.—Type material was designated by McCulloch (1914) but there is some ambiguity as to whether the syntypes are restricted to those three specimens specifically mentioned (McCulloch, 1914: 89) or if the other material (97 specimens from the same locality), which clearly contributes to the description, is included. Since these latter specimens were not specifically excluded from the type series I consider them name-bearing types and Schultz's (1961) designation of one of these as lectotype valid.

There has been much confusion associated with treatments of *P. tridentifer.* Many species of the *P. spinosus* species group have three large subequal posttemporal spines but this and *P. soelae* are the only ones with nondenticulate (note exceptions in description) ACB and denticulate ACC photophore clusters. Denticulation and pigmentation in *P. soelae* are very similar but median and ventral posttemporal spines are reduced.

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APPENDIX

Character Matrix.—Discrete-coded character states used in phylogenetic analysis using PAUP. The order of transformation is not indicated by the numerical sequences. Missing values indicated by '?'.

Argyripnus	000000000? 000?010?00 0000001000 ?001000??0 0?000?0?00
	0100???000 0010001000 00000?0?00 000?01?100 000000?0?0 000??00000 0000000000 000
Sternoptyx	000?000??0 000??10?00 000?00?000 0010011?00 0?000?0?10
	0000???000 00000000?0 1000000?0? 000?10?100 00000000?0 000??00000 1111111111 111
Argyropelecus	0000000??0 000?010100 ??0001?000 0001001?00 0?000?0?00
	0000??0000 0000000000 0000000?0? 000?10?1?0 0010000?0 001??00000 1111111111 111
ruggeri	1111111111 1121111111 1111110000 0000000000 0?000?0000
	00000?0000 0000000000 0000000?00 000?010100 00000000?0 000??00000 1111111100 000
meteori	1111111111 1121111111 1111110000 0000000000 0?000?0000
	00000?0000 0000000000 0000000?00 000?010100 00000000?0 000??00000 1111111100 000
matsubarai	1111111111 1121111111 1110000000 0000000000 0?000?0000
	00000?0000 0000000000 0000000?00 000?010100 00000000?0 000??00000 1111111100 000
kiwiensis	1111111111 1121111110 0000000000 0000000000 0?000?0000
	00000?0000 0000000000 0000000?00 000?010100 00000000?0 000??00000 1111111100 000
triphanos	1111111111 1000000000 0000001111 1000000000 0?000?0001
	00000?0000 0000000000 1000000?00 000?000100 00000000?0 000??00000 1111111100 000
laternatus	1111111110 1000000100 0000001111 1111000000 0?000?1100
	00000?0000 0000000000 0000000?00 000?000100 00000000?0 000??00000 1111111100 000
asteroides	1111111111 1000000000 0000001111 1111111100 0?000?0000
	00000?0000 0000000000 0000000?00 000?000100 00000000?0 000??00000 1111111100 000
clarus	1111111111 1000000000 0000001111 1111111100 0?000?0000
	00000?0000 0000000000 0000000?00 000?000100 00000000?0 000??00000 1111111100 000
polli	1111111111 1000000000 0000001111 1111111000 0?000?0000
	00000?0000 0000000010 0000000?00 000?000100 00000000?0 000??00000 1111111100 000
danae	1111110000 0030000000 0000000000 2000001011 1?111?1101
	11111?1101 1111111111 1000000?00 000?020100 00000000?0 000??00000 1111111100 000
unispinus	1111110000 0030000000 0000000000 2010011011 1?111?1111
	11111?1111 1111111111 1010000?00 000?1?0100 00000000?0 000??02000 1111111100 000

aquavitus 1111110000 0030000000 0000000000 2010000011 1?111?1110
1111?1110 0000000000 0000000?00 000?0?0100 00000000?0 000??00010 1111111100 000

omphus 1111110000 0000000000 0000000000 2010000011 1?111?1111
00000?0000 0000000000 0001000?00 000?010100 00000000?0 000??00000 1111111100 000

inermis 1101110000 0010000000 0000000000 2000010011 1?100?0000
00000?0000 0000000000 0111111?11 111?120011 0100101110 0000?00000 1111111100 000

nuttingi 1111110000 0010000000 0000000000 2000010011 1?100?0000
00000?0000 000000?000 0111111?11 111?121011 0000000000 0010?00000 1111111100 000

indicus 1111110000 0010000000 0000000000 2000010011 1?100?0000
00000?0000 0000000000 0111111?11 111?121011 1111000000 0000?00000 1111111100 000

asper 1111110000 0010000000 0000000000 2000010011 1?100?0000
00000?0000 0000000000 0111111?11 111?121011 1111110000 0000?00000 1111111100 000

paxtoni 1111110000 0010000000 0000000000 2000010011 1?100?1100
00000?0000 0000000000 0111111?11 111?121011 1111111001 0000?00000 1111111100 000

elongatus 1111110000 0010000000 0000000000 2000010011 1?100?1100
00000?0000 0000000000 0111111?11 111?121011 1101101001 1110?00000 1111111100 000

stereope 1111110000 0010000000 0000000000 2000010011 1?100?1100
00000?0000 0000000000 0111111?11 111?121111 1101101011 1111?10000 1111111100 000

spinifer 1111110000 0010000000 0000000000 2000010011 1?100?1100
00000?0000 0000000000 0111111?11 111?121111 1111111011 1111?01110 1111111100 000

soelae 1111110000 0010000000 0000000000 2000010011 1?100?1100
00000?0000 0000000000 0111111?11 111?121111 1110111011 1111?01111 1111111100 000

tridentifer 1111110000 0010000000 0000000000 2000010011 1?100?1100
00000?0000 0000000000 0111111?11 111?121111 1110111011 1111?01111 1111111100 000

ovatus 111111?111 11??11111? ???0??0000 ?00?00?000 ???0??00??
00??0?00?0 0?000?0??? ?000000??0 0?0?0?0100 00000000?? 0????000?0 ?111?1?10? 0??

bruuni 111111?111 10??00000? ???0??1111 ?10?00?000 ???0??00??
00??0?0??0 0?000?0??? ?000000??0 0?0?0?0100 00000000?? 0????000?0 ?111?1?10? 0??

oluolus 111111?110 00??00000? ???0??0000 ?00?01?011 ???0??00??
00??0?0??0 0?000?0??? ??11111??1 1?1?1?1000 000000000? 0??0?000?0 ?111?1?10? 0??

parini 111111?000 00??00000? ???0??0000 ?00?01?011 ???0??00??
00??0?00?0 0?000?0??? ?111111??1 1?1?1?1011 110111111? 0??0?000?0 ?111?1?10? 0??

fraseri 111?1????0 ?0??00000? ???0???000 ?00?01??11 ?????01??
00????00?0 0?000?0??? ?111111??1 1?1?1??0?1 1011?1101? 1??1?000?0 ?111?1?10? 0??

spinosus 111111?000 00??00000? ???0??0000 ?00?012011 ???0??11??
00??0?00?0 0?000?0??? ?111111??1 1?1?1?1111 110110101? 1??1?100?0 ?111?1?10? 0??